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## Population Ecology and Reproductive Biology of The Diamondback Watersnake, *Nerodia Rhombifer* (Serpentes: Colubridae), in Southernmost Texas

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POPULATION ECOLOGY AND REPRODUCTIVE BIOLOGY OF THE  
DIAMONDBACK WATERSNAKE, *NERODIA RHOMBIFER*  
(SERPENTES: COLUBRIDAE), IN  
SOUTHERNMOST TEXAS

A Thesis

by

RUBEN D. ZAMORA

Submitted to the Graduate School of the  
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Major Subject: Biology

POPULATION ECOLOGY AND REPRODUCTIVE BIOLOGY OF THE  
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December 2009

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## ABSTRACT

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*Nerodia rhombifer* is a polytypic, semi-aquatic snake with a broad geographical distribution ranging from the American Midwest southward to Chiapas, Mexico.

Although relatively abundant throughout much of its range, few ecological studies of the species have been conducted. This study provides basic population ecology information in a subtropical habitat. Population data were obtained in a mark-recapture study at Santa Ana National Wildlife Refuge, Hidalgo County, Texas, from August 1995 to December 1998. Specimens taken elsewhere in Hidalgo County provided information on the reproductive biology. This study provides the first absolute density estimates from anywhere within the species' range. Quantitative information on seasonal activity, growth rates, size dimorphism, population structure, reproductive cycles, and lipid dynamics are presented.

## DEDICATION

There are a handful of people who have touched my life very deeply. These individuals have and continue to inspire me to give my best. Without their sacrifices, this work would not have been possible. My daughters Julianna and Arianna surrendered the summer of their 5<sup>th</sup> and 7<sup>th</sup> years respectively so that I could finish what I started many years ago. My wife Melissa offered constant support and encouragement especially during the times that I felt like giving up. Andy, even before his birth, unknowingly showed me the value in continuing my formal education. Finally, I dedicate this thesis to my mom Odilia and dad Raul for displaying interest in my activities throughout all of my life. Mom could certainly hold her own brand of toughness while dad, a farmer and rancher, worked long hours in the field, but she never forgot to give a hug after the reprimands for my childhood mischief were over. I could not have asked for a better balance of toughness and tenderness, which I am ever more grateful for as I advance in age and parenthood. Dad certainly knew something about the natural and cultural history of the land he worked and made time to take me hunting and fishing. I can still remember him challenging me to hand-capture that checkered garter snake.

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Dr. F. W. Judd served as chair of my thesis committee until he retired in 2003. Afterwards he continued to serve as a committee member. His advice on all aspects of this study was invaluable. I am grateful for his commitment toward my academic growth and for sticking with me when I indicated that I wanted to finish what I started many years ago. Drs. R. I. Lonard and T. Brush also served on my thesis committee early on. Dr. Lonard made useful comments on the initial study proposal, but he also retired before the thesis was completed. I am indebted to Drs. R. Edwards and T. Brush for assuming committee positions left by the retirements of Drs. R. I. Lonard and F. W. Judd, respectively. Their suggestions for improvements on earlier versions of the thesis are greatly appreciated. I am especially thankful to Dr. Brush for taking on the administrative direction and leadership of my thesis committee.

E. Hopson, M. Bray, R. Gorena, M. Estrada, J. Mueller and numerous refuge volunteers supplied much needed help in the field. Special thanks to J. Judd for regular assistance running traps and data collection. J. Rupert produced the maps of the study area. M. Keck, M. Plummer and R. Aldridge graciously provided data on litter sizes. M. Sternberg estimated Willow Lake dimensions and gave directions for obtaining historical weather data. L. Narcisse gave me the opportunity to become skilled at various wildlife censusing techniques which directly lead to my interest in this study.

## TABLE OF CONTENTS

	Page
ABSTRACT.....	iii
DEDICATION.....	iv
ACKNOWLEDGEMENTS.....	v
TABLE OF CONTENTS.....	vi
LIST OF TABLES.....	viii
LIST OF FIGURES.....	x
CHAPTER I. INTRODUCTION.....	1
CHAPTER II. MATERIALS AND METHODS.....	5
<i>Study Sites</i> .....	5
<i>Population Sampling and Data Collection</i> .....	7
<i>Absolute Abundance</i> .....	8
<i>Relative Abundance and Seasonality</i> .....	9
<i>Population Structure</i> .....	10
<i>Biomass</i> .....	10
<i>Reproduction</i> .....	11
<i>Sexual Size Dimorphism</i> .....	12
<i>Growth</i> .....	14
<i>Lipids</i> .....	16



CHAPTER III. RESULTS .....	18
<i>Capture Frequencies</i> .....	18
<i>Absolute Abundance</i> .....	18
Relative Abundance and Seasonality.....	19
<i>Population Structure</i> .....	20
<i>Biomass</i> .....	22
<i>Reproduction</i> .....	22
<i>Sexual Size Dimorphism</i> .....	24
<i>Growth</i> .....	25
<i>Lipids</i> .....	26
CHAPTER IV. DISCUSSION.....	28
<i>Capture Frequencies</i> .....	28
<i>Absolute Abundance</i> .....	28
<i>Relative Abundance and Seasonality</i> .....	35
<i>Population Structure</i> .....	41
<i>Biomass</i> .....	44
<i>Reproduction</i> .....	45
<i>Sexual Size Dimorphism</i> .....	50
<i>Growth</i> .....	53
<i>Lipids</i> .....	56
CHAPTER V. CONCLUSIONS .....	61
LITERATURE CITED .....	111
BIOGRAPHICAL SKETCH .....	120

## LIST OF TABLES

	Page
TABLE 1. Summary of trapping effort for <i>Nerodia rhombifer</i> from Willow Lake at Santa Ana National Wildlife Refuge. ....	67
TABLE 2. Equations for the growth models tested for fit to growth increments collected on <i>Nerodia rhombifer</i> from Willow Lake at Santa Ana National Wildlife Refuge.....	68
TABLE 3. Summary of capture rates for <i>Nerodia rhombifer</i> over 31 monthly trapping periods at Santa Ana National Wildlife Refuge.....	69
TABLE 4. Comparison of population sizes generated using three different methods of estimation for mark-recapture data taken from a population of <i>Nerodia rhombifer</i> at Santa Ana National Wildlife Refuge. ....	70
TABLE 5. Mean snout-vent length (SVL) and mass for the sample used to construct size and age structures for <i>Nerodia rhombifer</i> from Willow Lake at Santa Ana National Wildlife Refuge.....	72
TABLE 6. Mean SVL and mass for specimens collected from irrigation canals in Hidalgo County, Texas. ....	73
TABLE 7. Female and litter characteristics for <i>Nerodia rhombifer</i> collected from irrigation canals in Hidalgo County, Texas. ....	74
TABLE 8. Female and litter size characteristics for four populations from subtropical, temperate and tropical regions. ....	75

TABLE 9. Size summaries for <i>Nerodia rhombifer</i> from Willow Lake, Santa Ana National Wildlife Refuge.....	76
TABLE 10. Summary of neonate sizes born to three female <i>Nerodia rhombifer</i> collected in Hidalgo County, Texas. ....	77
TABLE 11. ANOVA summaries examining sex and litter differences in neonate snout-vent length (SVL), neonate mass, and neonate tail length (TL) for three <i>Nerodia rhombifer</i> litters from Hidalgo County, Texas .....	78
TABLE 12. Regression equations and coefficients of determination for all five models fitted to growth data for <i>Nerodia rhombifer</i> from Willow Lake, Santa Ana National Wildlife Refuge.....	79
TABLE 13. Estimated growth as a percent of SVL per day (specific growth rate, G) and 95 % predicted limits (P.L.) for selected SVLs. ....	80
TABLE 14. Mean snout-vent length (SVL), body mass, and fatbody mass for male and female <i>Nerodia rhombifer</i> collected from Hidalgo County, Texas. ....	81

## LIST OF FIGURES

	Page
FIG. 1. Map of the study site displaying the location and arrangement of each of two trapping grids. ....	82
FIG. 2. Mass versus snout-vent length (SVL) for <i>Nerodia rhombifer</i> captured at Willow Lake, Santa Ana National Wildlife Refuge from August 1995 to December 1998. ....	83
FIG. 3. Size of Willow Lake <i>Nerodia rhombifer</i> versus date of capture.....	84
FIG. 4. (A) Monthly comparisons of the number of Willow Lake <i>Nerodia rhombifer</i> captured with expected values generated from trapping effort. (B) Monthly relative abundances for all Willow Lake <i>Nerodia rhombifer</i> represented as a percent of sample corrected for sampling effort. ....	85
FIG. 5. Monthly comparisons of the number of Willow Lake <i>Nerodia rhombifer</i> captured with expected values generated from trapping effort. ....	87
Fig. 6. Monthly relative abundances of Willow Lake <i>Nerodia rhombifer</i> represented as a percent of sample corrected for sampling effort for (A) juveniles, (B) adult females, and (C) adult males.....	89
FIG. 7. (A) Mean monthly photophase, and (B) mean total monthly precipitation and mean monthly temperatures for years 1995-98. ....	91
FIG. 8. Size structure for <i>Nerodia rhombifer</i> constructed from data collected from Willow Lake, Santa Ana National Wildlife Refuge from 1995-1998. ....	92

FIG. 9. Mass structure for <i>Nerodia rhombifer</i> constructed from data collected from Willow Lake, Santa Ana National Wildlife Refuge from 1995-1998. ....	93
FIG. 10. Age structure for <i>Nerodia rhombifer</i> constructed from size data collected from Willow Lake, Santa Ana National Wildlife Refuge from 1995-1998. ....	94
FIG. 11. Sex ratios for individual adult <i>Nerodia rhombifer</i> by month from Willow Lake, Santa Ana National Wildlife Refuge. ....	95
Fig. 12. (A) Size of reproductive structures for female <i>Nerodia rhombifer</i> $\geq 75.5$ cm SVL collected in irrigation canals in Hidalgo County, Texas. (B) Mean mass of testes for male <i>Nerodia rhombifer</i> $\geq 48.4$ cm SVL collected in irrigation canals in Hidalgo County, Texas. ....	96
FIG. 13. Comparison of regression lines of litter sizes versus maternal snout-vent lengths (SVL) for <i>Nerodia rhombifer</i> from Hidalgo County, Texas and three other populations from temperate and tropical regions. ....	97
FIG. 14. Comparison of common slope models and marginal mean SVLs for Hidalgo County, Texas <i>Nerodia rhombifer</i> and three other populations from temperate and tropical regions. ....	98
FIG. 15. Comparison of the regression lines of tail length (TL) versus snout-vent length (SVL) between male and female <i>Nerodia rhombifer</i> from Willow Lake, Santa Ana National Wildlife Refuge. ....	99
FIG. 16. Comparison of the regression lines of log(Mass in grams) versus log(SVL in cm) between male and female <i>Nerodia rhombifer</i> from Willow Lake, Santa Ana National Wildlife Refuge. ....	100

FIG. 17. A graphical comparison of mean neonate size by maternal female size for both male and female neonates for three <i>Nerodia rhombifer</i> litters from Hidalgo County, Texas. ....	101
FIG. 18. Regression lines by sex for the differential forms of the (A) power, (B) logistic, and (C) Gompertz growth models fit to growth data for <i>Nerodia rhombifer</i> from Santa Ana National Wildlife Refuge. ....	102
FIG. 19. Growth curves generated by integrating the regression equations estimated from field growth rates of female and male <i>Nerodia rhombifer</i> from Willow Lake, Santa Ana National Wildlife Refuge. ....	103
FIG. 20. The relationship between fatbody mass (FBM) and snout-vent length (SVL) for (A) adult male ( $N = 52$ ) and (B) adult female ( $N = 42$ ) <i>Nerodia rhombifer</i> collected in Hidalgo County, Texas. ....	104
Fig. 21. The relationship between fatbody mass (FBM) and body mass (BM) for (A) adult male ( $N = 52$ ) and (B) adult female ( $N = 41$ ) <i>Nerodia rhombifer</i> collected in Hidalgo County, Texas. ....	105
FIG. 22. Residual index versus fatbody index for (A) adult male ( $r = 0.955$ , $N = 52$ , $P < 0.001$ ) and (B) adult female ( $r = 0.964$ , $N = 42$ , $P < 0.001$ ) <i>Nerodia rhombifer</i> collected in Hidalgo County, Texas. ....	106
Fig. 23. Fatbody index (FBI) calculated for (A) adult male ( $N = 52$ ) and (B) adult female ( $N = 42$ ) <i>Nerodia rhombifer</i> collected in Hidalgo County, Texas. ....	107
FIG. 24. Fatbody index (FBI) by month for (A) adult male ( $N = 52$ ) and (B) adult female ( $N = 42$ ) <i>Nerodia rhombifer</i> collected in Hidalgo County, Texas. ....	108

FIG. 25. Comparison of monthly relative abundances among four geographically distinct populations of <i>Nerodia rhombifer</i> ranging from tropical Mexico to the northeastern Texas. ....	109
FIG. 26. Survivorship curves for <i>Nerodia rhombifer</i> from Willow Lake at Santa Ana National Wildlife Refuge. ....	110

## CHAPTER I

### INTRODUCTION

The diamondback water snake *Nerodia rhombifer* is a polytypic species consisting of three subspecies inhabiting the United States and Mexico. Two subspecies, *N. r. blanchardi* and *N. r. werleri*, are limited in geographic range to Mexico. The former occurs in the states of Nuevo Leon, Tamaulipas, San Luis Potosi, Hidalgo, and Veracruz, and the latter occurs in Veracruz, Tabasco, Campeche, and Chiapas (Conant, 1969). Intergrades between *N. r. blanchardi* and *N. r. werleri* occur in central Veracruz (Conant, 1969). *Nerodia r. rhombifer* is the only subspecies that occurs in the United States and is the only representative of its genus to occur naturally in the lower Rio Grande Valley (LRGV) of Texas. The Florida water snake (*N. fasciata pictiventris*) is a non-native, accidental introduction to the LRGV and is limited to the Brownsville, Texas area (Tennant, 1984). *Nerodia r. rhombifer* ranges from central Indiana westward to western Kansas and southward to southernmost Alabama through the eastern two-thirds of Texas into Mexico (Conant and Collins, 1991). In Mexico, *N. r. rhombifer* occurs in the states of Coahuila, Nuevo Leon, Tamaulipas (Conant, 1969). Intergrades between *N. r. rhombifer* and *N. r. blanchardi* occur from the Rio Salinas in Nuevo Leon (Conant, 1969).

Field identification of *N. r. rhombifer* is determined by a network of rhombi on the dorsum which are outlined by blackish brown scales. The rhombi intersect with



similar-colored lateral vertical bars. The background color is light olive-brown. The eyes have round pupils and the iris may be red or orange. The ventral side is yellow and randomly marked with blackish crescents. There are 25 to 31 strongly keeled, mid-body rows of dorsal scales and a divided anal plate. This non-venomous, semi-aquatic colubrid has an uncanny musking ability and will bite vigorously when molested (Tennant, 1984; Vermersch and Kuntz, 1986; Conant and Collins, 1991).

*Nerodia rhombifer* generally occurs below 500 m elevation (Keck, 2004) and inhabits almost any permanent, non-urban body of water including lakes and ponds, rivers, streams, marshes, and man-made reservoirs (Tennant, 1984; Vermersch and Kuntz, 1986; Keck, 2004). This snake also may be found in water hazards on golf courses, irrigation canals and drainage ditches (pers. obs.; Conant, 1969). Individuals most commonly occur along gently sloping ( $< 45^\circ$ ), sparse to densely vegetated shorelines or resting on woody vegetation hanging above water (Cagle, 1937; Preston, 1970; Hebrard and Mushinsky, 1978; Keck, 1998). In irrigation canals, *N. rhombifer* may be most abundant among riprap associated with water control structures where they forage and bask (pers. obs.). Compared to other watersnakes, *N. rhombifer* is highly aquatic but usually stays within 2 m of the shoreline (Hebrard and Mushinsky, 1978; Keck, 1998), although individuals have occasionally been observed moving on land (Keck, 2004)

Throughout much of its range, *N. rhombifer* may be the most abundant semi-aquatic snake (Cagle, 1937; Conant, 1969; Hebrard and Mushinsky, 1978; Keck, 1994). This may be due to the ability of this snake to persist in borderline habitats (Tennant, 1984), e.g., borrow and drain ditches along suburban and agricultural areas (pers. obs.).

Despite relatively high abundances and a broad geographic distribution, little is known regarding the ecology of *N. rhombifer*, and studies have been conducted in only a few regions (Keck, 2004). While food habits and reproduction in *N. rhombifer* have been well documented (e.g., Betz, 1963; Mushinsky and Hebrard, 1977; Plummer and Goy, 1984; Aldridge et al., 1995), population structure and biomass have not been reported, and with the exception of one paper on litter size from extreme south Texas (Judd and Bray, 1996) there has been no study of subtropical populations of *N. rhombifer*.

Because this species is an intermediate predator, it may be a major trophic link in aquatic ecosystems. With the increasing threats to biodiversity associated with an exploding human population, it has become ever more important to provide basic information on wildlife populations such as distribution, abundance, and reproduction. As wetland ecosystems have and continue to suffer enormously from various human activities (Zedler and Kercher, 2005), information on *N. rhombifer* populations should be invaluable to management and conservation matters where this species and associated biological communities occur (Dodd, 1993).

The goal of this study is to fill the void in natural history information for *N. rhombifer* in the subtropical region of its geographic range. Specifically, an estimate of population density is provided using mark-recapture techniques at Santa Ana National Wildlife Refuge which borders the lower Rio Grande. From the mark-recapture field data set, patterns in seasonal abundance, population structure, sex-related size dimorphism, and size-specific growth are described. Snakes were collected outside of the refuge to examine reproduction. This data set provides information on the onset and termination of reproduction, litter, neonate and maternal female size, and size at maturity

for males and females. Litter sizes are compared with other populations and coelomic fatbodies are examined for lipid cycling.

## CHAPTER II

### MATERIALS AND METHODS

*Study Sites.*—Field data for the population study were collected on Willow Lake at Santa Ana National Wildlife Refuge (SANWR) located in southernmost Hidalgo County, Texas, U.S.A. (26.0795°N, 98.1395°W, 25 m elev.). This 845-hectare (2088 acre) refuge borders the Rio Grande and is situated in a region known as the Matamorán Biotic District of the Tamaulipan Biotic Province (Blair, 1950). While some 95% of the regional native flora has been replaced by agriculture and urban development, the remaining plant life within the river floodplain is composed of a mixture of thornscrub, thorn forest, riparian forest, and wetlands (Jahrsdoerfer and Leslie, 1988). The climate in this region may be classified as subtropical and semiarid (Lonard et al., 1991).

The plant communities within the refuge range from riparian and bottomland hardwoods dominated by cedar elm (*Ulmus crassifolia*), anacua (*Ehretia anacua*), sugar hackberry (*Celtis laevigata*), and Rio Grande ash, *Fraxinus berlandieriana* (Vora, 1990; Lonard and Judd, 2002) to dry, open shrublands with mesquite (*Prosopis glandulosa*), Texas torchwood (*Amyris texana*), coma (*Bumelia celastrina*), spiny hackberry (*Celtis pallida*), black brush (*Acacia rigidula*), and cenizo, *Leucophyllum frutescens* (Vora, 1990). The variety of these habitats corresponds to differences in topography, soil, and flood regime (Vora, 1990).

Since the 1950s, the seasonal flooding that once occurred along the Rio Grande floodplain has been completely interrupted with the construction of upstream dams. Consequently, as has been observed in other regulated river systems (Nilsson and Berggren, 2000), the remaining plant communities which depended on the historic seasonal overflow of the Rio Grande are threatened. Wetland management on SANWR has included pumping well water into three main pools, including Willow Lake (Vora, 1990), delivering water from a larger network of irrigation canals outside the refuge, pumping water directly from the adjacent portion of the Rio Grande, and periods of drawdown to control invasive plant species.

Vora (1990) described the three shallow ponds at SANWR. These ponds and other depressed areas where bottomland forests occur are old oxbows (or resacas) of the Rio Grande. When flooded, the three ponds are colonized by various submergent, emergent, and floating aquatic plants (Vora, 1990). During drawdown periods, densely growing emergents such as cattails (*Typha domingensis*) and bulrush (*Schoenoplectus pungens*) are removed to prevent complete invasion of these ponds. The habitats surrounding Willow Lake resemble the former resaca bottoms and seasonally flooded plant communities described by Vora (1990). The north side is bordered by a Rio Grande ash, sugar hackberry, and cedar elm. The remainder is fringed by sugar hackberry, huisache (*Acacia smallii*), Rio Grande ash, and retama (*Parkinsonia aculeata*).

Irrigation canals and associated drainage ditches transect much of Hidalgo County. These irrigation canals serve to deliver water from the Rio Grande for agriculture use and municipalities. Grasses and forbs grow along the banks and fringes of the canals above the bank slopes. Trees including willow (*Salix* sp.), sugar hackberry,

huisache, and retama sometimes establish above the water line along with emergents such as cattail and bulrush. This vegetation is periodically cleared to prevent backup of drainage during storms. The network provides pathways where some wildlife including *N. rhombifer* can disperse and migrate (pers. obs.). Specimens for the reproduction study were collected in these canals.

*Population Sampling and Data Collection.*—Population sampling was conducted using mark-recapture techniques. Snakes were captured using funnel traps (Fitch, 1951) arranged into two trapping grids (Fig. 1). The grids were erected on Willow Lake at SANWR. The traps were run for two consecutive days at biweekly intervals from 30 August 1995 to 18 December 1998. Because of logistical problems, sampling effort was interrupted twice. Consequently, only 61 trapping periods were conducted (Table 1).

The grids were established using 2.5 cm PVC pipes (stakes). The stakes were arranged into rows ten meters apart. Within each row, the stakes were placed at ten meter intervals. The first grid was made up of five rows, each with six traps. It was placed on the southeastern corner of impoundment #3 of Willow Lake with the long side parallel to the southern shoreline. The grid had a total area of 0.20 hectares. The second grid had three rows with seven traps each and was established on the northeast corner of impoundment #4. The long side was parallel to the northern shoreline and had a total area of 0.12 hectares.

The funnel traps were constructed of 6-mm mesh hardware cloth. The bodies of the traps were cylindrical and measured 100 cm long × 26 cm diameter. Two funnels constructed of the same material with a 5-cm opening were fitted to each end of each of

the trap bodies. The funnels made the lengths of the traps about 160 cm. To allow snakes access to air at the surface, traps were attached to the grid stakes with hose clamps and s-hooks permitting adjustment as water levels increased or decreased. Clamps were adjusted to have no more than 80% of the trap cylinder submerged.

At initial capture, individual *N. rhombifer* were marked with passive integrated transponders (PIT tags; Gibbons and Andrews, 2004). The PIT tags were implanted subcutaneously with a syringe and 12 gauge modified needle on the right side of the snake, anterior to the vent. The tags were each composed of a microchip encased in a glass capsule measuring  $10 \times 2.1$  mm. The mass of the tag was 0.6 g and the microchip had a unique preprogrammed code which was read by a scanner. The code allowed for identification of individuals upon recapture.

For individual captures and recaptures during each sampling period, the location of capture, PIT tag number, sex, snout-to-vent length (SVL), total length (ToL), and mass were recorded. Capture locations were identified by uniquely numbered traps. Sex was diagnosed following the description of dimorphism by Conant and Collins (1991) and the method of Gregory (1983) for young snakes. The SVL is measured from the tip of the rostrum to the posterior edge of the anal plate, and ToL is obtained by measuring the entire length of the snake. Meteorological data were secured from the NOAA tables for the nearest two weather stations located in Weslaco and McAllen, Texas.

*Absolute Abundance.*—Absolute abundance estimates were calculated using three methods: minimum numbers alive (MNA), Schnabel, and Jolley-Seber (Krebs, 1998). Because capture frequency was low and because individuals were observed to move from

one grid to the next in a relatively short period of time, capture data for both grids were combined. The capture data were arranged into a Method B table (Krebs, 1998) on a spreadsheet which was then used to calculate the population sizes and confidence intervals (except for MNA which is a direct enumeration). In addition, the full Jolly-Seber model was explored by formatting data into coded capture histories and importing the data into the program JOLLY (Pollock et al., 1990). The program provides a goodness-of-fit test and was accessed from the Patuxent Wildlife Research Center software archive (Hines, 1988)

*Relative Abundance and Seasonality.*—Relative abundance was calculated by dividing the number of individuals captured per month, and per season, by the trapping effort. Thus, by this definition, relative abundance is defined as the capture frequency which assumes that the number of captures in a given period with a given effort is proportional to the number of snakes using the grids. For convenience, the number of trapping periods in a given time period was used as a measure of trapping effort instead of number of trap-days. Using the total number of individuals captured and trapping effort per month and per season, expected capture rates were calculated. To examine seasonal patterns, the expected capture frequencies were compared against the observed capture frequencies using chi-square goodness of fit tests (Sokal and Rohlf, 1995). Correlation analyses also were employed to study the relative strengths in the relationships between abundance estimates and physical environmental factors including photoperiod, air temperature, and water temperature. To facilitate comparisons of seasonal patterns of abundance among populations, monthly relative abundances were converted to percent relative abundances.



*Population Structure.*—Capture records and growth rates were used to construct size and age structures at SANWR. As with abundance estimates, data across years were combined. However, because this analysis examines the structure of the population at a given time, within the limitations of this study (i.e., low capture rates), defined as individuals present in a calendar year, recaptures within a year were not counted but among years were. For individuals that were captured more than once within a year only the first capture record was used. Sex ratios were calculated for the entire study period. To detect any seasonal changes in sex ratios, data from all years were pooled and examined by season. Six seasons were observed: early spring (February-March), late spring (April-May), early summer (June-July), late summer (August-September), fall (October-November), winter (December-January). Six seasons were used to better resolve potential changes in sex ratios among seasons throughout a calendar year. Individuals recaptured within the same season of a given year were only counted once but were counted again if recaptured later. All sex ratios generated were tested for unity (i.e., not different from 1:1) using a chi-square test according to recommendations of Sokal and Rohlf (1995) when there is only one degree of freedom.

*Biomass.*—Biomass was calculated for each month using the mass structure and population density values computed from the Jolly-Seber abundance estimates for each sampling period. The average mass for the overall mass structure was multiplied by each density estimate. The biomass values were converted to units of kg/ha to facilitate comparisons with literature values.

*Reproduction.*— Males and females were collected monthly from several sites in Hidalgo County, Texas. Most sites were part of the network of irrigation canals and included one reservoir. The sites ranged from 1.5 km N (26°05'34.67" N, 98°08'09.52" W, 25 m elev.) to 34 km N (26°23'1.23" N, 98°09'44.62" W, 27 m elev.) of SANWR. Additional snakes were taken from other sites when opportunity arose, e.g. accidental deaths from the mark-recapture efforts described above. Snakes were collected with minnow traps similar to those described above or more often by hand. Date and location of capture were recorded for each specimen collected.

Only snakes no less than 10 cm below the minimum size at maturity reported for either sex (Aldridge et al., 1995) or greater were kept. Specimens were kept frozen in the lab until necropsies could be performed. Gravid females were held in the lab and given water and food ad lib until parturition. Date of birth and sizes (mass, SVL, and tail length, TL) of the female and neonates were recorded. Sex for neonates was determined by manual eversion of the hemipenes (Gregory, 1983).

The mass of males and females was determined to the nearest tenth of a gram with an OHAUS® triple beam balance with animal container. Total length and SVL were measured to the nearest millimeter. Sex specific data were recorded. For males, the following data were recorded: (1) the mass, length and width of each testis and (2) the presence or absence of spermatozoa in the ductus deferens as determined by opaqueness (Shine, 1980a). The following data were obtained for females: (1) the masses and lengths of the right and left ovaries described as being from the oviductal infundibulum to the posterior limit of the kidneys by Betz (1963); (2) the number of vitellogenic follicles in preovulatory ovaries; (3) the number oviductal eggs or embryos for each ovary and

oviduct of postovulatory females; and (4) the lengths of the ten largest ovarian structures in preovulatory females or ten largest oviductal structures in postovulatory females.

The length and seasonality of reproductive activity for both sexes was determined by observing the months for which the respective gonads show reproductive condition. An estimate of the frequency of reproduction in females was determined by dividing the number of reproductively active females (those showing vitellogenesis, containing oviductal eggs or embryos, and displaying signs of recent parturition) by the sample size from the dates during which reproductive activity was observed. To investigate the relationship between female size and litter size, litter size was regressed against female SVL. Because litter size varied with female size, an analysis of covariance (ANCOVA) using female size (SVL) as the covariate was used to determine the relationship of this trait among subtropical, temperate, and tropical populations (Aldridge et al., 1995).

*Sexual Size Dimorphism.*—Because maximum size may be an indicator of relative size among species of water snakes (Gibbons and Dorcas, 2004), the same may be true among populations and between sexes within a population. To examine sexual size dimorphism (SSD) for body length, the upper quartile values for SVL for males and females were compared using a Mann-Whitney U test. This test assumed that all individuals had an equal probability of being captured. According to Case (1976) such comparisons among populations may be less sensitive to age structure than comparisons of means or medians for the populations being considered.

In general, North American watersnakes display SSD for tail length (TL) with males having proportionally longer tails (Gibbons and Dorcas, 2004). To ascertain the

extent of SSD for TL for this south Texas population, TL was plotted against SVL for each sex and because this scatter plot indicated that TL varied linearly with SVL for both males and females, an ANCOVA using SVL as the covariate was employed to determine the degree of the difference in TL between the sexes.

In the field, adult female *N. rhombifer* appeared broader in body form than did males of comparable SVL. To investigate SSD for this character, mass was used as a proxy for body form. Mass was plotted against SVL for both sexes and compared. The scatter plot showed slightly different positive curvilinear relationships (Fig. 2). To determine if there was a difference in this relationship between the sexes, mass and SVL were log-transformed and the log of mass in grams was regressed against the log of SVL in centimeters for both sexes. A plot of the slopes of the regression lines comparing females and males suggested that the slopes were not homogenous, a violation of ANCOVA assumptions. The slopes were checked for homogeneity with the general linear models (GLM) procedure using sex (the independent variable) by logSVL (the covariate) as the interaction term.

Neonates were also examined for SSD for SVL, TL, and mass. Five neonates were stillborn (1 female and 3 males) or underdeveloped (1 individual, sex undeterminable). The underdeveloped, and unsexed, neonate was left out of the analysis for SSD. Because TL and mass in neonates also vary with SVL as for the older cohorts, an ANCOVA using SVL as the covariate also was used to examine differences between TL and mass between sexes. But because the maternal female (i.e., litter origin) may also influence neonate size, a two-level mixed model ANOVA (Quinn and Keough, 2002) was employed treating sex as the fixed factor and litter as a random effect. Snout-vent-

length was used as a covariate for the analyses of TL and mass. Treating litter as a random effect allows for inferences to be made about the population (King et al., 1999).

*Growth.*—Growth rates (GR) were calculated as the change in snout-vent-length (SVL) in centimeters divided by the time interval between capture in days (Van Devender, 1978). Occasionally, individuals captured more than once apparently decreased in size giving negative values for growth rates. This was most likely due to error in measurement of SVL. Because the power growth model (see below) requires that all growth rates are positive, negative growth rates were eliminated from the analysis described below. This assured that all models were compared with the same bias.

For some individuals that were captured three or more times, consecutive growth rates for a capture history of an individual were calculated. While this might represent a sort of temporal pseudo replication (Cox, 1996), doing this allowed more opportunities to measure growth rates for different sizes. Another measure of growth, the specific growth rate (G), also was calculated for all time intervals for each capture history as was done for GR. Specific growth rate is the GR divided by size. This value is equivalent to an estimate of percent increase in size per day (Kaufmann, 1981). Values for G were estimated according to Kaufmann's recommendation, where

$$G = \frac{(\ln SVL_2 - \ln SVL_1)}{\Delta t} \quad \text{Equation 1}$$

Cross-sectional growth data, i.e. observations of growth for many individuals of different sizes, were used to examine differences in growth rate between males and

females. It has been shown that such data can be used to represent, on average, the growth trajectories for individuals in a population (Marvin, 2001). Since growth rates for many organisms are functions of size, cross-sectional GR values were plotted against the algebraic mean SVL ( $\overline{SVL}$ ) during the time interval in which the change in SVL was observed (Van Devender, 1978). The same was done for G except that the average size was calculated as the geometric mean of  $SVL_1$  and  $SVL_2$  (hereafter referred to as S). Further, G was also plotted against certain transformation of S. The curves of all plots, when properly fit as a straight line, describe a different schedule at which growth rate decreases. These different schedules are more commonly represented as one of several integrated growth curves (Van Devender, 1978; Kaufmann, 1981). The advantage of using these differential equations (Table 2) is that it allows one to determine which growth curve best fits the data. Further, it allows a comparison of growth curves of different treatments with simple linear regression techniques (Van Devender, 1978; Kaufmann, 1981). Using these techniques, all models were plotted to determine the best fit growth model. The best fit models were then used to compare growth rates between males and females using an ANCOVA with  $\overline{SVL}$  or S, depending on the model being analyzed, as the covariate.

Integrated growth models were constructed for each sex using the parameters estimated from the best fit differential models (Kaufmann, 1981). The relationship between the estimated parameters and the integrated growth models are presented in Table 2. A well fit integrated model could be useful for estimating age of an individual if size is known (Cox, 1996); however the age at a specific size must be known when fitting these models. Size at birth could be conveniently assigned an age of zero ( $t = 0$ ). While

the size of neonates can be estimated from neonate data, no growth data were collected for neonates in this study. The mean SVL for the growth increment of the smallest male captured was 34.7 cm and 40.2 cm for females. Therefore, the fitted models only describe growth for males and females greater than or equal to the respective values.

An obstacle to fitting an integrated growth model to data from this population was that age was not known for any individuals. A plot of size versus date of capture (Fig. 3) suggests that the size of neonates and juveniles captured at Willow Lake were similar to those reported by Scudder-Davis and Burghardt (1996). Therefore, the size ranges reported for one year-old males and females (Scudder-Davis and Burghardt, 1996) indicate that the ages for the smallest male and female captured at Willow Lake were approximately 365 days.

*Lipids.*—During the necropsies, coelomic fatbodies were removed, dried with paper towels and massed to the nearest 0.001 g. Regression analyses revealed that fatbody mass (FBM) varied positively with body size (SVL and body mass, BM). Typically, an ANCOVA using body size as a covariate would be appropriate for group comparisons of FBM, however the assumptions of equal slopes and homogenous variances among groups did not hold even after various transformations of the variables. An alternative for controlling for the influence of a covariate is to compare group variances of the residuals from a regression between covariates (in this case FBM and BM), referred to as a residual index. Another involves calculating an index by dividing each variant by the respective covariant, e.g. percent FBM by BM. Garcia-Berthou (2001) and Packard and Boardman (1999) discussed the flaws in both techniques that lead to systematic statistical errors. Of

particular problem in the latter technique is that the underlying assumption that the two variables are isometric is often violated (Packard and Boardman, 1999). Thus a plot of the index versus the covariate would have a slope that differs from zero indicating allometry. Such a case occurs when log-log plot reveals an allometric coefficient of 1 but the intercept is not 1, i.e. when the relationship is linear but the intercept is not the origin. This was the case when FBM was regressed against BM for both sexes.

Because there was still a need to control for the effect of body size on FBM for group comparisons, an index was calculated but with consideration of the allometric relationship between FBM and BM. For males and females separately, a fatbody index (FBI) was calculated for each variant by first subtracting the value of the respective regression intercepts from FBM before dividing by BM. These index values were arcsine transformed and checked for normality within groups and homogenous variances among groups before means were compared. When these assumptions were violated, non-parametric comparisons of central tendency were employed.



## CHAPTER III

### RESULTS

*Capture Frequencies.*— Since snakes freely moved from one grid to the other, in some cases the next day, data for the two grids were combined. Between August 1995 and December 1998, a total of 61 trapping periods were conducted (Table 1). This was equivalent to 6222 trap·days ( $61 \text{ periods} \times 2 \text{ day}\cdot\text{period}^{-1} \times 51 \text{ traps}$ ). During this time a total of 254 captures were recorded, for a capture rate of 4.2 snakes per period, or 0.041 snakes per trap day. Because capture rates were relatively low, capture data were pooled for each month. Individuals that were captured more than once in a month were not counted as recaptures since the entire month was considered the sampling period. This reduced the number of captures to a total of 232, but increased the mean capture rate to 7.5 snakes per period (calculated for 31 periods; Table 3). Of the 232 captures, a total of 78 were recaptured at least once for a recapture rate of 2.5 snakes per period. Thus 154 individuals were handled at least once ( $232 \text{ captures} - 78 \text{ recaptured individuals}$ ).

*Absolute Abundance.*—The Schnabel, Jolly-Seber, and MNA methods of estimating population size for the 0.32 ha combined grid area generated markedly different results for the same mark-recapture data set (Table 4). Overall, the Schnabel method produced the highest values, while MNA produced the lowest values. The cumulative average estimated number of individuals using the Schnabel method was 194.4 and ranged from

85 individuals in September of 1995, to 250.0 in July of 1998. In general, the Schnabel estimates increased with time. The average estimated number of individuals with the Jolly-Seber method was 47.6 individuals and ranged from 5.0 in October of 1998, to 115.7 in August of 1996. These estimates appeared to vary irregularly displaying peaks in March, August, and November. The average MNA was 14.5 and ranged from three in October 1998, to 30 in August 1996. The MNA values peaked and dipped similarly to Jolly-Seber estimates. Although Schnabel population size estimates generally increased from 1996 to 1998, the Jolly-Seber population size estimates were strikingly lower in 1998 than in the previous two years (Table 4).

*Relative Abundance and Seasonality.*—Monthly capture rates for all individuals were significantly different from expected captures generated from trapping effort (Fig. 4A;  $\chi^2 = 97.2$ ,  $df = 10$ ,  $P < 0.001$ ). Thus relative abundances deviated significantly from an even distribution in most months (Fig. 4B). When the sample was divided by age and sex, mean monthly captures were significantly different from expected captures generated from trapping effort for juveniles (Fig. 5A;  $\chi^2 = 25.2$ ,  $df = 4$ ,  $P < 0.001$ ), adult females (Fig. 5B;  $\chi^2 = 53.3$ ,  $df = 8$ ,  $P < 0.001$ ), and adult males (Fig. 5C;  $\chi^2 = 40.5$ ,  $df = 8$ ,  $P < 0.001$ ). Thus relative abundances of these three groups deviated significantly from an even distribution in most months (Figs. 6A, B, and C). Further, there were differences among the cohorts in how abundance was distributed among months (Figs. 6A, B, and C).

The four-year monthly averages for total precipitation and temperature (Fig. 7) varied somewhat from the 40 yr averages reported by Lonard et al. (1991). The average

annual temperature was 0.64 °C higher and average total annual precipitation was down 12.81 cm during the four-year period. Correlation analyses revealed strong relationships between relative abundance and mean monthly air temperature ( $r = 0.897$ ,  $N = 12$ ,  $P < 0.001$ ) and mean monthly photoperiod ( $r = 0.851$ ,  $N = 12$ ,  $P < 0.001$ ), but not mean total monthly precipitation ( $r = 0.311$ ,  $N = 12$ ,  $P = 0.326$ ). Multiple regression analysis did not reduce error below that predicted by mean monthly air temperature alone, probably because photoperiod was colinear with air temperature. While precipitation was not colinear, partial correlation after holding air temperature constant was not significant ( $r = 0.004$ ,  $df = 9$ ,  $P = 0.991$ ).

*Population Structure.* —Only 175 capture records fit the conditions to be included in the population structure analyses. Thus 21 records come from individuals that were recaptured in at least one other calendar year and counted in the snapshot of the population structure for that year (Table 5). The results from combining the snapshots from all years follow.

The sex of 13 juveniles was either not known or not recorded (Fig. 8). Of the individuals that were sexed, the majority of males captured in traps (approximately 85%) were between 55.0 and 95.0 cm (Fig. 8). No males were observed in categories greater than 95.0 cm. In contrast, captured females were distributed somewhat evenly among the size categories ranging from 45.0 to 115.0 cm (Fig. 8). Approximately 47% of females were between 55.0 and 95.0 cm, and almost 30% of females were greater than 95.0 cm. Of the 13 individuals not sexed, 11 were young of the year as they were less than 35 cm and captured between 25 July and 17 October. The mass structure (Fig. 9) shows that

females had a broader range of masses and attained much greater masses than did males. The largest female was 3.7 times the mass of the largest male (Table 5), although no attempt was made to separate gravid from no-gravid females. Approximately 86% of males and 37% of females had masses ranging from 101-500 g. While one male was just greater than 500 g, approximately 45% of females attained such masses.

An age structure (Fig. 10) was generated based on power growth models (see *Size and Growth* below). The age structure suggests that approximately 55% of all individuals captured were one and two year olds. Only 3% of males and 23% of females were greater than five years old. Individuals less than one year old likely were underrepresented making up only 5% of the sample. Even when the 11 unsexed juveniles less than 35 cm SVL are added, young of the year make up only about 11% of the sample. Thus all proportions in this age class analysis are biased against the greater weight of the 0-1 year old age class.

Sex was determined for 142 of 154 individuals captured. Sixty-one individuals were recorded as male and 81 individuals were recorded as female. This ratio, while favoring females, did not differ from unity ( $\chi^2 = 2.54$ ,  $df = 1$ ,  $P = 0.111$ ). When excluding juveniles from analysis, a ratio of 58 individual adult males to 69 individual adult females was observed which did not differ from unity ( $\chi^2 = 0.787$ ,  $df = 1$ ,  $P = 0.375$ ). A separate analysis of those juveniles that were sexed ( $n = 25$ ) showed that the sex ratio (7M:18F) was weakly female biased ( $\chi^2 = 4.00$ ,  $df = 1$ ,  $P = 0.046$ ). When all records including recaptures were combined, males were captured on 105 occasions and females were captured on 128 occasions. The overall male to female capture ratio did not differ from unity ( $\chi^2 = 2.27$ ,  $df = 1$ ,  $P = 0.132$ ).

When sex ratio is examined by month (Fig. 11), slightly more individual males were observed in April and May, and more individual females were observed in August and September. The sex ratio in August was significantly skewed in favor of females ( $\chi^2 = 7.042$ ,  $df = 1$ ,  $P = 0.008$ ). When captures were pooled by season excluding recaptures within a season, the overall male to female ratio was 99:124 and did not differ from unity ( $\chi^2 = 2.80$ ,  $df = 1$ ,  $P = 0.094$ ). When the pooled data were examined by season, only the ratio in late summer (August-September) was significantly female biased (15M:37F,  $\chi^2 = 8.48$ ,  $df = 1$ ,  $P = 0.004$ ). In all other seasons, the ratios did not differ from unity ( $P \geq 0.487$  for other seasons).

*Biomass.*— The average mass used to determine biomasses for each sampling period was 396.3 g/snake. Biomass values ranged from 0.3 kg/ha in October 1998, to 6.4 kg/ha in August 1996. The average biomass calculated from individual biomass values for each sampling period was 2.60 kg/ha. As expected, biomass for Willow Lake *N. rhombifer* varied with density (Table 4), thus the values are apparent and related to snake activity in the trapping grids.

*Reproduction.*— Seventy-one females and 54 males were collected for the reproductive study (Table 6). Of these individuals, 21 females displayed some form of reproductive activity (i.e., had enlarged follicles, oviductal eggs or embryos, or evidence of recent parturition in the uterus) and 53 males had sperm in the ductus deferens. Reproductive females ranged from 75.5 to 112.7 cm SVL and 494.0 to 1564.5 g, while mature males ranged from 51.8 to 78.8 cm SVL and 86.1 to 481.4g.

Three litters were born in the lab to females ranging from 83.0 to 89.0 cm SVL; birth dates were from 19 July to 12 September (Table 7). Litter sizes were 12, 14, and 17, and overall female to male sex ratio was 20:22 ( $\chi^2 = 0.024$ ,  $df = 1$ ,  $P = 0.877$ ). The sex for one underdeveloped neonate was not determinable. For the three litters combined, the mean neonate size ( $\pm 1$  SE) was  $22.4 \pm 0.32$  cm SVL (range: 17.3-25.0 cm) and mean neonate mass ( $\pm 1$  SE) was  $9.05 \pm 0.32$  g (range: 3.10-11.57g).

Enlarging follicles were observed as early as 27 May, oviductal eggs as early as 31 May, and oviductal embryos as early as 28 June. Vascular spots in the uterus were observed as late as 30 September, which is likely a conservative date for the termination of the reproductive season (Fig. 12A). Males showed an increase in average testicular mass from mid-August to late October and perhaps into November (Fig. 12B). This indicated that spermatogenesis in males occurred while females were still gravid or giving birth.

The three litters born in the lab and the dissections of 14 females provided estimates of litter size. The average litter size ( $\pm 1$  SE) for Hidalgo County, Texas was  $15.4 \pm 2.03$  ( $N = 17$ ) and ranged from four to 39. The average female size ( $\pm 1$  SE) was  $91.66 \pm 2.912$  cm SVL. Litter size was strongly correlated with female SVL ( $r = 0.721$ ,  $N = 17$ ,  $P = 0.001$ ). Despite female *Nerodia rhombifer* from Hidalgo County being larger in SVL compared to populations from east-central Texas, and Veracruz, Mexico, but not Arkansas, mean litter size ranked lowest (Table 8). A general linear model (GLM) procedure testing for the interaction between female SVL and location among populations indicated that the slopes of the regressions of litter size versus female SVL were homogenous (Fig. 13;  $F_{3,55} = 1.59$ ,  $P = 0.202$ ). After controlling for female SVL,

there was a significant difference in litter size among populations (ANCOVA:  $F_{3, 58} = 6.98$ ,  $P < 0.001$ ). Pairwise comparisons of the marginal means for litter size suggested that *N. rhombifer* from the south Texas population had significantly smaller litter sizes than both the Arkansas and Veracruz populations, but not the east-central Texas population (Fig. 14).

*Sexual Size Dimorphism.*—For size comparisons, if an individual was captured more than once only the first capture was used to meet the assumption of independence. On average, females were larger than males for both SVL and mass but not TL (Table 9), but because population structure may influence comparisons of means while investigating sexual size dimorphism, comparisons of upper percentiles may be more instructive (Case, 1976). A Mann-Whitney U test indicated that the upper-quartile female SVL, (median = 106.0 cm, range = 97.3-120.0 cm,  $N = 19$ ) were significantly greater than that for males (median = 82.0 cm, range = 76.8-93.5,  $N = 16$ ;  $U = 0$ ,  $P < 0.001$ ).

Tail length and SVL were positively correlated for both females and males (Fig. 15). After controlling for the effects of SVL, males had significantly greater TLs than did females (ANCOVA:  $F_{1, 135} = 16.07$ ,  $P < 0.001$ ). Mass and SVL were strongly correlated for both sexes after log transforming the data (Fig. 16). However, the slopes of the regression lines were not homogenous (GLM interaction term sex\*SVL:  $F_{1, 134} = 4.75$ ,  $P = 0.031$ ), indicating that females gained mass at greater rates than did males.

For three litters born in the lab (Table 10), there was a significant influence of maternal female on neonate SVL, but SVL did not differ between sexes (Table 11). A graphical analysis showed a tendency for larger females to produce both larger male and

female offspring (Fig. 17). There were strong positive correlations between neonate SVL and neonate TL ( $r = 0.840$ ,  $N = 42$ ,  $P < 0.001$ ) and between SVL and mass ( $r = 0.937$ ,  $N = 42$ ,  $P < 0.001$ ). Neonate mass and neonate TL also were strongly influenced by maternal female (as expected from proportional relationships between these measures of size and SVL), but after accounting for both SVL and maternal female effects, only TL was significantly different between the sexes (Table 11); males had longer TLs (Estimated Marginal Means ( $\pm 1$  SE) for TL at 22.6 cm SVL: male =  $6.95 \pm 0.055$  cm, female =  $6.21 \pm 0.067$  cm).

*Growth.* —The power model best fit the growth data, while the Von Bertalanffy models explained the least amount of variation associated with size related growth rates (Table 12). Because of a violation of the assumption of independence (some repeated measures were used) the regression lines were not compared to make formal inferences about growth rates between males and females. Although there was no significant difference in growth rates,  $\ln G$ , between males and females after controlling for size,  $\ln S$  (ANCOVA:  $F_{1,64} = 2.141$ ,  $P = 0.148$ ), considering that growth rates were highly variable, the regression lines suggest that females grew faster at a given size than males and that the rates decreased with increasing size (Fig. 18). Nonetheless the top three models were integrated for visual comparisons (Fig. 19). Since only the power growth curves were used to construct the age structure above (Fig. 10), only those equations are provided: Fig 19A; females:  $S(\text{in mm}) = [8.405\text{E}6(\text{Age (in days)} - 320.9)]^{3.368^{-1}}$ ; males:  $S(\text{in mm}) = [6.106\text{E}6(\text{Age (in days)} - 309.5)]^{3.373^{-1}}$ . The equations for the other growth curves can be constructed using the relationships between the regression



coefficients and the respective differential and integrated growth equations (Tables 2 and 12). All growth curves show that females grew at faster rates than males. The growth rates for males declined more rapidly, diverging from females at between 1 and 2 years of age. The asymptotic growth rates for males occurred at approximately 93 cm and 102 cm for the logistic and Gompertz curves respectively (Fig. 19B and 19C). For females, a rapid decrease in growth occurred at about 2.5 years of age for all curves, but the logistic and Gompertz models approached asymptotic growth at approximately 106 cm and 111 cm, respectively (Fig. 19B and 19C).

Because specific growth rate ( $G$ ) is considered to be a percent increase in size per day (Kaufmann, 1981), the associated regression equations from Table 12 can be used to estimate this parameter. This was done for the power model. As expected from the regression coefficients, females grew at faster rates measured as a percent of body length than males at comparable sizes and both male and female specific growth rates decreased with size (Table 13).

*Lipids.*— Females were significantly larger and had significantly more fat stored in body cavities than males ( $P < 0.001$  for all comparisons; Table 14). In males ( $N = 52$ ), fatbody mass (FBM) was positively correlated with both SVL ( $r = 0.487$ ,  $P < 0.001$ , Fig. 20A) and body mass ( $r = 0.689$ ,  $P < 0.001$ , Fig. 21A). Females also showed positive relationship between FBM and both SVL ( $r = 0.438$ ,  $N = 42$ ,  $P = 0.024$ ; Fig. 20B) and body mass ( $r = 0.636$ ,  $N = 41$ ,  $P < 0.001$ , Fig. 21B).

The fatbody index (FBI) was strongly correlated to the residual index from the regression of FBM against body mass (BM; Fig. 22), therefore FBI appeared to

adequately control the effects of body size on FBM. Scatter plots of FBI by date showed that FBI values for males were generally lower in spring but began to increase by mid-summer (Fig. 23 A). Quiescent and reproductive females did not appear to have a discernable pattern although data for spring and mid- to late-fall were limited (Fig. 23 B). When FBI values were grouped by month, differences in FBI values among months were significant for males (Kruskal-Wallis test:  $\chi^2 = 21.70$ ,  $df = 7$ ,  $P = 0.003$ ; Fig. 24 A) but not for females (Kruskal-Wallis test:  $\chi^2 = 8.78$ ,  $df = 7$ ,  $P = 0.269$ ; Fig. 24 B).

## CHAPTER IV

### DISCUSSION

*Capture Frequencies.*—While there was an overall recapture rate of approximately 33% (range = 0 - 100%), the actual number of captures per sampling period was low (mean = 7.7, range = 0 - 19). Six of the periods had no captures and half of all trapping periods had no more than five total captures. Such low rates of capture appear to be common among studies of snake populations. Parker and Plummer (1987) cite reduced “tractability” when compared to studies involving other types of animals. They mention four factors for this reduction which include often being inconspicuous and nocturnal, having inactive periods, low apparent densities, and displaying irregular and extensive movements. Sampling aquatic snakes may add an additional dimension of lessened tractability as their habitat is a virtually hidden, three-dimensional space. For example, using a similar method of trapping as in this study, Keck (1998) had a return of just 12% of 284 semi-aquatic snakes that were originally marked. The snake species in his samples in order of decreasing capture frequency included *N. rhombifer*, *Nerodia erythrogaster*, *Nerodia fasciata*, and *Agkistrodon piscivorus*.

*Absolute Abundance.*—The population size estimates (Table 4) likely have bias, low precision, or both. To better explain the bias in the Schnabel estimate, it may be easier to view all mark-recapture estimates as being based on the Lincoln-Peterson method: the

proportion of marked animals in a subsequent sample,  $\frac{m_2}{n_2}$ , is directly related to the proportion of all animals previously marked in the population,  $\frac{m_1}{N}$  (Greenwood, 1996).

Thus,

$$\hat{N} = \frac{m_1 n_2}{m_2} \quad \text{Equation 2}$$

If capture rates are low, especially recapture rates as in other snakes (Parker and Plummer, 1987), the population size estimates,  $\hat{N}$ , will be positively biased.

The Schnabel estimates generally increased over the study period from August 1995 to November 1998, probably because of recruitment by way of births (or at least individuals moving up into the catchable population) and migration was likely. Quite simply, the snakes from the Willow Lake population were moving into and out the trapping grids from throughout the lake. Given a reasonably sized population, it may be that more unmarked snakes immigrated into the grid than emigrant-marked snakes were reentering. Since the Schnabel model does not provide for losses with replacement in study populations (definition of a closed population), recruitment before a sampling period would continue to decrease the ratio of marked to unmarked snakes in each of the subsequent samples over the duration of the study. Assuming that the probabilities of natural mortality for both marked and unmarked snakes are the same, which would not affect the estimation (Hayne, 1949; Krebs, 1998), the decreasing ratio would cause the observed increase in the Schnabel estimates over time. Emigration away from not just the trapping grids but from Willow Lake entirely, while less likely for *N. rhombifer* than for other semi-aquatic snakes (Hebrard and Mushinsky, 1978; Keck, 1998), would have

the same effect as natural mortality unless marked animals are more likely to emigrate or emigrants are replaced from outside. In which case, the result would further dilute the number of marked animals available for recapture and also cause a positive and increasing bias in consecutive estimates.

The bias associated with the population size estimates discussed for the Schnabel method should be removed with the Jolly-Seber method since it is designed for open populations (Krebs, 1998). For a series of at least three trapping periods, the bias is handled by the addition of an estimate of the number of individuals marked in the population at the time of sampling ( $\hat{M}$ ). The estimated number of marked animals includes three new terms: the number of animals marked and captured before a sample but not captured until a future sample is taken ( $z$ ), the number released at the time of sampling ( $R$ ), and the number of released from the current sample (i.e.,  $R$ ) of which a number ( $r$ ) are subsequently captured. The estimate is calculated as follows:

$$\hat{M} = \frac{zR}{r} + m \quad \text{Equation 3}$$

And the Jolly-Seber population size estimate is then,

$$\hat{N} = \frac{n\hat{M}}{m} = \frac{nzR}{mr} + n \quad \text{Equation 4}$$

In Equations 3 and 4,  $n$  and  $m$  are the same as  $n_2$  and  $m_2$  from Equation 2. The difference is that the number marked previously,  $m_1$ , is now replaced with the estimate  $\hat{M}$ . This adjustment allows for flux in the proportion of marked animals which occurs in

real (open) populations. Thus the Jolly-Seber estimates for *N. rhombifer* in Table 4 should be unbiased assuming that all individuals have an equal probability of being captured, an assumption of all mark-recapture estimators mentioned (Jolly and Dickson, 1983). While the Jolly-Seber population estimates here may be free of bias, there is virtually no confidence in them as the percent relative precision (Greenwood, 1996) for the population estimates ranged from 118-1600%. The extremely broad confidence limits are a consequence of small sample sizes that result in large standard errors for population estimates (Parker and Plummer, 1987).

The reason for the significant decrease in the Jolly-Seber population size estimates for 1998 is not entirely clear (Table 4). However, during the mid-1990s, the region suffered a string of drought years. Because local waterways such as resacas, irrigation canals, and wetlands are artificially flooded from reservoirs upstream from the portion of the Rio Grande that borders southern Hidalgo County, *N. rhombifer* populations are not likely to suffer significantly during dry years. But, as competition for dwindling reservoir water increased during the mid-1990s, local water authority restrictions caused Willow Lake to dry up in late 1997. Consequently, trapping effort was halted by September 1997. It is likely during this period that individuals of the Willow Lake *N. rhombifer* population either migrated or perished. Indeed, one previously marked individual from Willow Lake was captured approximately 500 m away in a low laying pond (Pintail Lake) that still contained water during the intermission. This may help explain the significant drop in Jolly-Seber population estimates when Willow Lake was again flooded and trapping resumed in March 1998.

The MNA has no estimate of precision because it is an enumeration method. Jolly and Dickson (1983) have shown that the use of MNA as a measure of population size will consistently provide underestimates. At best, when catchability is high MNA approaches the true population size (Krebs, 1998). The Jolly-Seber population estimate  $\hat{N}$  will be equal to MNA when the following condition is met:  $u = R - r = 0$ ; where  $u$  is the number of unmarked individuals in the sample (Jolly and Dickson, 1983). Thus from Equation 4, when  $m = n$  and  $R = r$ ,  $\hat{N} = z + n = \text{MNA}$ . This may be illustrated with tortoises which may be considerably more catchable than snakes. In a population study of the Texas tortoise *Gopherus berlandieri* (Judd and Rose, 1983) all five MNA values reported were negatively biased (percent difference range: 0.60 – 43%), however four of the five annual estimates had a percent difference of less than 19%. In contrast, all but one of 28 monthly MNA values for this *N. rhombifer* population were more than 40% lower than the Jolly-Seber estimates (percent difference range: 0 – 87%). The one exception was in December 1996, when no snakes were captured despite 204 trap-days of effort that month. In this case, MNA was equal only to  $z$ , i.e. previously marked snakes that were later captured in subsequent trapping periods. Thus in December 1996, at least 12 snakes were known to be alive even though there was no apparent activity in the trapping grids.

The biases and low precisions of the population estimates for *N. rhombifer* in this study (Table 4) limit their use for species management or studies involving population and community dynamics. Caution should be taken when using these reported values to calculate density and biomass, not only in recognizing the errors previously discussed but also recognizing that the study area is greater than that of the two grids as individuals

regularly moved into an out of the grids. Using merely the areas of the grids will most likely introduce a positive bias inflating density values (Krebs, 1998) and further confound the interpretation of the original abundance estimates.

There are four lines of evidence that justify both combining the data from the two grids (see methods) and using the area that makes up all the impoundments of Willow Lake to estimate the density for the *N. rhombifer* population. First, snakes readily moved from one grid to the next. Of 154 individuals that were recaptured, 23 were captured at least once in each of the grids. Four were recaptured in the other grid the very next day. Four individuals were captured in one grid, then recaptured in the other grid, and then recaptured again in the original grid of capture. Second, the total area of the of Willow Lake is approximately 7.2 ha which is just above the upper home range limit reported by T. Michot for *N. rhombifer* in Louisiana (Keck, 2004). Keck (2004) also reported a mean range length (maximum distance between any two points) of 678 m. Third, other investigators reported that *N. rhombifer* was typically found no greater than 2-3 m away from the water (Diener, 1957; Hebrard and Mushinsky, 1978; Keck, 1998). Lastly, in this study, there were 155 captures recorded in rows 3, 4, and 5, with offshore distances—perpendicular from the main grid axes—of about 20, 30, and 40 m, respectively, suggesting that snakes were not limited to near shore water.

Conceptually, the entire lake can be viewed as a large cauldron in which marked snakes mixed back into the population. As snakes went about their activities during trapping periods, the grids acted as a sieve in which random samples of the mixture were taken. Because there is no evidence to suggest that snakes were not using the entire area of Willow Lake or to a significant degree were not restricted to the area of Willow Lake



where the traps were located, the most conservative density estimate should then use the entire area (7.2 ha) of Willow Lake. A less cautious density estimate would use only the areas of the impoundments where the trapping grids were located, approximately 5.5 ha.

Using the most conservative value for the size of study area, the maximum density for *N. rhombifer* at Willow Lake is 16.1 snakes/ha (Table 4). The one attempt at estimating density for *N. rhombifer* from Louisiana was reported as a linear density of 180.7 snakes/km (Hebrard and Mushinsky, 1978). Because the value is given as a linear density and some details regarding the application of the population estimation method were left out, it is difficult to make comparisons. However, given the description of the Louisiana study site and using the same rationale in determining the study area above (see also Fig.2 of Laurent and Kingsbury, 2003: 27% of *N. rhombifer* were observed > 15 m offshore), the linear density estimate converts to a true density estimate of 24.1 snakes/ha, a value slightly higher than the Willow Lake population.

There are few reports on the densities for snakes of the genus *Nerodia* (Gibbons and Dorcas, 2004), probably because of the difficulty in obtaining adequate capture-recapture data. However, Brown and Weatherhead (1999) estimated values of 25 and 28 individuals/ha for *N. sipedon* which are comparable to 24.1 snakes/ha (calculated from Hebrard and Mushinsky, 1978) and the maximum estimate of 16.1 snakes/ha for this study. In contrast, Fitch (2000) reported a density of 0.30 individuals/ha for *N. sipedon* from Kansas and King et al. (2006) reported a median density of 141 individuals/ha (range: 11-1107 individuals/ha) for the Lake Erie watersnake, *N. sipedon insularum*, representing extreme density values for the genus. Of the density estimates reviewed by Parker and Plummer (1987) for 57 snake populations, half were  $\leq 5$  individuals/ha of

which almost three quarters were  $\leq 1$  individual/ha. Thus the maximum density estimated for Willow Lake *N. rhombifer* in this study of 16.1/ha is well above the median. However, higher densities have been reported for other snakes including those mentioned above for *N. sipedon*, 20 individuals/ha for tiger snakes *Notechis scutatus* (Bonnet et al. 2002), 107 individuals/ha for the plains gartersnake *Thamnophis radix* (Stanford and King, 2004), 430 individuals/ha for the rough green snake *Ophedrys aestivus* (Plummer, 1985), and 1289 individuals/ha for the striped crayfish snake *Regina alleni* (Godley, 1980).

*Relative Abundance and Seasonality.* —Because capture rates may be considered indices of relative abundance and short-term changes in abundances are often influenced by activity patterns (Parker and Plummer, 1987; Willson et al., 2008), the observed capture rates for *N. rhombifer* at Willow Lake strongly suggest that activity varied significantly among months (Figs. 4A and 5A-C). However, the activity pattern was not apparent from absolute numbers of monthly captures until they were corrected for monthly sampling effort (Table 1). For adult and juvenile *N. rhombifer* combined, activity appeared to have two peaks, one in late spring-early summer and the other in early fall (Fig. 4B). Thus, *N. rhombifer* from Willow Lake may exhibit a slightly bimodal activity pattern, one of two typical activity patterns seen in temperate zone snakes such as *Heterodon* spp. and *Virginia valeriae* (Gibbons and Semlitsch, 1987). Interestingly, other semi-aquatic snakes belonging to the closely related genera *Regina* and *Seminatrix* as well as congeners may exhibit a unimodal pattern with most activity occurring in spring and early summer (Gibbons and Dorcas, 2004). However, *Seminatrix pygea* from

South Carolina may also have a bimodal activity pattern, though data collection from this population occurred only during one field season (Winne et al., 2005). Indeed, inter-year variation in relative abundances can influence attempts to describe activity patterns in snake populations. For example, in this study, in September of 1995 *N. rhombifer* were captured at a rate of 0.17 snakes/trap-day but in September of 1998 *N. rhombifer* were captured at 0.024 snakes/trap-day, an apparent 7-fold drop in activity. The reason for such a drastic change in relative abundance is not clear but highlights the importance of considering the duration of sampling regimen when generalizing activity patterns for populations using capture frequencies.

When comparing geographically distinct populations of *N. rhombifer* specifically, there appears to be no pattern in peak activity with latitude (Fig. 25). There were two major peaks in activity for the tropical Veracruz population (Manjarrez and Garcia, 1991), the first in April and the second in June. For subtropical south Texas, activity appears to initially peak in May, but remains high through September. In Ascension Parish, Louisiana, *N. rhombifer* displayed a pronounced peak of activity in July (Mushinsky et al., 1980), while in Titus County, Texas peak activity appeared to happen earlier in June (Keck, 2004). In all populations, activity apparently decreases precipitously by early to mid-autumn and remains low through winter and early spring. The unusual peak in September for Hidalgo County, Texas (this study; Fig. 25) may be at least in part due to several neonates occurring in the September samples (Fig. 3), however even when all juveniles were excluded and adults examined separately a second peak in activity still remained in September. Therefore, *N. rhombifer* from extreme south Texas

may have an extended and sustained period of peak activity as measured by relative abundance.

The comparisons of seasonal activity among populations may be confounded by biases associated with sampling techniques (Keck, 1994), yearly variation in climatological factors (Manjarrez and Garcia, 1991), and seasonal changes in behavior of subpopulations (Fitch, 1987). For example, while not the objective of their study, the peaks in activity observed by Manjarrez and Garcia (1991) occurred during the dry season when water pools were drying, concentrating the fish the watersnakes were preying upon. Further, the two peaks calculated in Fig. 25 were the result of averaging two years of data collected by the investigators in which the peak abundance shifted from July in one year to April in the next. The authors attributed this change in peak activity to annual variation in temperatures and water levels (Manjarrez and Garcia, 1991). Thus the bias here resulted from major changes in available habitat to the population making among season comparisons of abundance within the population and among the other three populations of *N. rhombifer* (Fig. 25) difficult.

In comparing the three other populations *N. rhombifer* from the United States (Fig. 25), there is evidence that suggests that the use of funnel traps to sample semi-aquatic snakes may be biased to sampling foraging snakes as the traps can become naturally baited (Keck, 1994; Winne, 2005). However, even if snakes are engaged in other activities associated with fitness such as basking or mate searching (Gibbons and Semlitsch, 1987), separating the behaviors on the time scale in which the naturally baited traps mechanically sample snakes may not cause biases that would affect comparisons of seasonal activity patterns. For example, springtime males that may forego foraging to

search for mates may actively pursue foraging females into traps (cf. Zamora and Valadez, 2007). Indeed, multiple snakes of both sexes were captured in individual traps on several occasions during sampling. Furthermore, individual *N. rhombifer* have been observed basking while others are foraging (pers. obs.).

With respect then to these possible biases, although the *N. rhombifer* population from Hidalgo County in this study and the population from northeastern Texas were sampled with naturally baiting funnel traps while the population from Louisiana was sampled by active searches (thought to favor capture of basking snakes by Gibbons and Dorcas, 2004), any biases associated with either technique should not influence relative abundances so long as the techniques were systematically used throughout the respective studies. Therefore, the differences in activity patterns discussed above as measured by relative abundances should represent actual disparities among the three populations at least for the years in which the respective populations were sampled. The extended period of activity and bimodality seen in south Texas *N. rhombifer* were strikingly similar to other snakes from the Everglades National Park, Florida (Dalrymple et al. 1991), an area with a similar subtropical climate to south Texas.

Although *N. rhombifer* was not captured in January and December in some studies including December for this one (Fig. 25), other authors have anecdotally reported this species to be active throughout the year (Aldridge et al., 1995; Tu and Hutchison, 1995). Vermersch and Kuntz (1986) wrote that in Bexar County of south-central Texas this snake has been observed basking on branches a few feet above water in mid-winter when air temperatures were above 21.7 °C. This is consistent with the generalization that species which hibernate for long periods of time in the coldest regions

of their range may hibernate for shorter periods in warmer areas, even becoming intermittently active during the cold season (Gregory, 1982). It seems reasonable then that the lack of captures in this study for December was due to reduced activity in the cooler months coupled with low capture rates in the trapping grids (Table 3).

Of the meteorological variables examined, temperature explained the most variation (80.4%) in activity for Willow Lake *N. rhombifer*. Photoperiod also explained a significant amount of variation (72.4%) in activity. The difference in explanatory power may be due to lag in air temperature change when compared to change in photoperiod (Fig. 7). This strong influence of temperature on activity in reptiles is well documented (Gregory, 1982) and likely due to environmental constraints on the ability of snakes to regulate body temperatures that optimize important activities such as digestion, reproduction, predatory escape, and growth (Lillywhite, 1987). It is important to point out that the correlations between relative abundance and the meteorological variables were performed on average values across years for each month thus dampening annual variation in activity patterns. When the data were reanalyzed by year, temperature explained only 36.1% of the variation in relative abundance highlighting inter-year variation in activity. Thus, within years there is much unexplained variation in activity which may be due in part to the limitations of the sampling design (2 to 5 field days/month), especially as snake activity can vary greatly from day to day within a season (Brown and Shine, 2002).

That precipitation had no apparent influence on this population should not eliminate this factor from consideration especially in areas that experience wet and dry seasons (Reynolds, 1982; Manjarrez and Garcia, 1991; Brown et al. 2002). Historically,

before anthropogenic influence, the local hydrologic cycle which included overflows of the Rio Grande may have had a strong influence on *N. rhombifer* abundance. On a broad time scale, though, the extended activity period for Willow Lake *N. rhombifer* may be most influenced by shorter and milder winters.

The activity patterns varied among subpopulations. All groups showed dips in activity in July or August (Fig. 6A-C). The general causative factors for this reduction are not clear as any risk from reaching upper thermal tolerance limits are reduced by the apparent nocturnal activity of *N. rhombifer* (Mushinsky et al., 1980). However, the peaks for each group may be explained by differences in the types of activities occurring within each group. Most of the activity for juveniles should be associated with acquiring energy for growth. The increased peak in late summer and early fall is at least in part due to the inclusion of young of the year in the samples for August and September (Figs. 3 and 6A). This has been observed for other viviparous snakes (Dalrymple et al., 1991). In northeastern Texas, Keck (2004) also observed greater than expected numbers of juvenile *N. rhombifer* during July-September, although statistical significance was observed only in mid-summer. As mentioned earlier, this also helped contribute to the second peak activity for the overall Willow Lake population (Figs. 4B and 25).

The peak for adult females in May and relatively sustained activity until September (Fig. 6B) are consistent with female *Nerodia* continuing to feed throughout the reproductive season (Aldridge and Bufalino, 2003). For specimens collected for the reproductive study outside of the refuge, three reproductive females, one vitellogenic, one with oviductal eggs and one with embryos, had food items. While this constituted a

small percentage (20%) of reproductive females sampled, the individuals were collected by hand while active and presumably foraging.

Adult male *Nerodia rhombifer* were more bimodal in activity than adult females and reached peak activity in April, at least a month before females (Fig. 6B and C). The earlier activity is presumably due to aphagic male mate searching (i.e., non-feeding males regardless of proximate factors but correlated to mating activity) at the start of spring activity followed by resumed feeding later in the active season (Gibbons and Semlitsch, 1987; O'Donnell et al., 2004). It is interesting that Willow Lake male *N. rhombifer* were readily captured during the months of April and May (Fig. 6C) when mating is reported to occur (reviewed by Keck, 2004; Zamora and Valadez, 2007). Conversely, Winne (2005) observed an underrepresentation of males in early spring samples of funnel-trapped *S. pygaea*. He hypothesized that the funnel traps, which become naturally baited (Keck, 1994; Winne, 2005), were biased toward capturing foraging females and that males were foregoing feeding to search for females. If this is true and male *N. rhombifer* do not take food during the breeding season, then male *N. rhombifer* may be more likely to pursue foraging females into traps than male *S. pygaea*. There may be, of course, other possibilities to explore in both cases; male pursuit of females into traps provides a possible solution to this inconsistency.

*Population Structure.* —Other than a few accounts of sex ratios, there are no reports detailing population structure for *N. rhombifer*. This may be due in part to the difficulty in sampling all age groups, especially juveniles, which are typically underrepresented from field captures (Parker and Plummer, 1987). This was true for this study as at most



10% of the sample was made up of young of the year (including the 11 unsexed juveniles). This was due at least in part to the funnel traps themselves which have been shown to have increased escape rates for smaller snakes either through the funnel opening or directly through the mesh from the hardware cloth used to construct the traps (Willson et al. 2005). Indeed one such event was observed when a neonate became stuck in the mesh because of the bulge in the abdomen from a recently ingested prey item. There was, however, no reason to suspect that the traps used in this study were excluding larger class sizes from sampling (cf. Willson et al., 2008). Therefore, all size groups greater than young of the year cohort were assumed to be captured roughly according to their proportion in the population.

The difference in size distributions between female and male Willow Lake *N. rhombifer* (Figs. 8 and 9) was expected as members of this genus exhibit female biased sexual dimorphism (Gibbons and Dorcas, 2004). The extent of this dimorphism for Willow Lake *N. rhombifer* is discussed below. Ecologically, this difference is significant. Including juveniles, females made up approximately 75% of the population biomass. Even if more juveniles were captured, this estimate would probably not change much. Thus, female watersnakes are significant in contributing to productivity, probably serving as important links in matter cycling and energy flow in the Willow Lake ecosystem (Pough, 1980). As with other snakes, the size differences allow for the exploitation of different food sources (Mushinsky, 1987). Because juvenile, male and the larger female *N. rhombifer* may partition food by size (Kofron, 1978; Plummer and Goy, 1984; Manjarrez and Garcia, 1991), size may dictate where these subpopulations forage (Mushinsky et al., 1982). The small number of juveniles observed during sampling could

also be partially explained if traps were not placed in areas where juveniles regularly seek prey.

The age structure for Willow Lake *N. rhombifer* (Fig. 10) reflects the paucity of juveniles in samples, however assuming that proportion of individuals assigned to each age group by the sex-specific growth curves (see below) is representative of a relatively stable population over the four years of field work some useful information may be inferred. Using the further assumption that yearly survivorship rates are constant at ages  $\geq 1$ , the inverse mortality rates can be estimated with simple exponential decay (Fig. 26). The data suggest that after age 1 is reached, annual mortality rates are higher for males (56%) than for females (30%). Overall, the annual mortality rate is high at 45%, thus annual survivorship is low. This and other data associated with reproduction and growth are consistent with demographic characteristics exhibited by other early-maturing colubrids: low adult survivorship, low longevity, short cohort generation time, high fecundity, and annual reproduction (Parker and Plummer, 1987). Although information on population structures for *Nerodia* species is limited (Gibbons and Dorcas, 2004), the age structure for Willow Lake *N. rhombifer* appears to agree well with the age structure reported for a population of *N. sipedon* from Kansas (Fitch, 2000) suggesting similarities in mortality schedules. Because juveniles from age group 0-1 yr are likely underrepresented in the sample the mortality rates presented here are probably underestimates. Thus annual survivorship may be lower.

The overall primary sex ratio for the three litters born in the lab did not differ from unity (Table 7). The secondary sex ratios varied somewhat depending on the way the sample was broken down. In examining the total number of individuals captured

throughout the study (excluding any records of recapture) no significant differences were found for the entire population (61M:81F) or for adults only (58M:69F). While neither was significant, the slightly female-favored overall secondary sex ratios may be due to higher mortality rates from males (Fig. 26). The skewed sex ratio in August (Fig. 11) was due to greater activity of females compared to males. Alternatively, males displayed greater increases in activity in beginning in early spring (April-May) while female increases lagged until May-June (Figs. 6B and C). The earlier increases in male activity are echoed by the shift in male to female sex ratios from  $> 1.0$  in April and May to  $< 1.0$  in June (Fig. 11), but these differences were not significant. The early spring activity for males is likely due to mate searching (Gibbons and Semlitsch, 1987). Such early male activity has been observed in another population of *N. rhombifer* (Keck, 2004). But the reason for the abrupt decline in male activity in August that led to a female biased sex ratio for that month is not readily apparent.

*Biomass.* —Explanations for the proximate factors influencing variability in densities among populations discussed above are largely absent. Nevertheless, better insight may be gained by examining biomass and secondary productivity. The maximum biomass calculated for the Willow Lake population of *N. rhombifer*, 6.4 kg/ha, ranks among some of the highest values available for snake populations. Iverson (1982: Table 2) reviewed estimates of biomass for 38 snake populations; the maximum was 4.6 kg/ha. Other high biomass estimates include 6.3 kg/ha for *N. scutatus* (calculated from Bonnet et al. 2002), 7.1 kg/ha for *O. aestivus* (Parker and Plummer, 1987), and 30 kg/ha for *R. alleni* (Godley, 1980). At the other extreme, some snake populations may have standing crops one to

two orders of magnitude lower (see Fitch, 2000). Among the likely proximate factors influencing the unusually high density and biomass for *R. alleni* include extraordinarily high primary productivity, its trophic position and its relation to highly abundant prey, nearby alternative exploitable habitats, and reduced competitive and predatory pressures (Godley, 1980).

With exception of herbivorous mammals, the maximum biomass for Willow Lake *N. rhombifer* exceeds that of other mammals and all birds reviewed by Iverson (1982). Ultimately, such a high biomass is to be expected as ectothermic vertebrates have lower energy requirements and comparable, if not higher, productivity rates than most endotherms (Pough, 1980). The population structure for Willow Lake *N. rhombifer* (see above) is typical of early maturing colubrids with high mortality rates (Parker and Plummer, 1987). Assuming a stable population, this would suggest a relatively high population turnover requiring a necessarily high productivity. While the density estimate on which the biomass calculation is based is preliminary, it appears that, *N. rhombifer* plays a significant role in shaping ecosystem dynamics at Willow Lake.

*Reproduction.*— Distinguishing between mature and immature females was somewhat problematic, because corpora lutea (both during pregnancy and lingering, as described by Betz, 1963) were difficult to identify. This may have been due to freezing and extended cold storage of specimens. Consequently, the identification of reproductive females was based on individuals with vitellogenic follicles, oviductal eggs or embryos, females that gave birth, or females that displayed a distended uterus with reddish spots (herein referred to as uterine spots) which were assumed to be recently post-parturient. The

uterine spots were considered to be areas of increased vascularization associated with the site of attachment of embryonic membranes to the lumen of the uterus as seen in *S. pygaea* (Sever et al. 2000). Litter sizes were determined by counting all oviductal eggs, embryos, neonates, both live and dead (Gregory et al., 1992), and number of uterine spots acknowledging that overestimation may be possible with all structures except for neonate counts (Bonnet et al., 2008).

The smallest reproductive female *N. rhombifer* in this study (75.5 cm SVL) was within the range reported for populations from Arkansas (78.5 cm: Plummer, 1992), northeastern Texas (71.8 cm: Keck, 2004), Louisiana (68.8 cm: Kofron, 1979), and Veracruz (67.0 cm: Aldridge et al., 1995). The smallest reproductive male at Willow Lake was 51.8 cm SVL. This individual was markedly larger than the smallest males reported for northeastern Texas (49.8 cm SVL: Keck, 2004) and Veracruz (47.5 cm SVL: Aldridge et al. 1995).

The data from female reproductive tracts and from litters born in the lab suggested that there is a clearly defined season (Fig. 12A). Taking the period from late May when vitellogenesis was observed to late September when the last post-parturient female was collected, 21 out of 30 females greater than 75.5 cm SVL (or 70% of this sample) were reproductive. This proportion is likely an underestimate as some of the smaller females used in the analysis may delay their initial reproductive effort by a year (cf. Ford and Seigel, 1994). For example, Plummer (1992) found for an Arkansas population that although the smallest reproductive female was 78.5 cm SVL, only 56% of females between 79.0-85.0 cm SVL were reproductive, but those > 85.0 cm SVL were all

reproductively active. Thus, reproduction for Willow Lake females appears to be annual as in other *Nerodia* (e.g., *N. cyclopion*: Kofron, 1979; *N. sipedon*: King, 1986).

The onset of vitellogenesis for Willow Lake *N. rhombifer* in spring is difficult to tell from the data set as no individuals were collected between 14 April and 23 May (Fig. 12A). However, females may be receptive as early as the first week of April (Meade, 1934; Zamora and Valadez, 2007). They are beginning to increase activity in April (Fig. 6B), and the general progression in the lengths of ovarian and oviductal structures suggest that the process of follicular enlargement begins in early to mid-April. This agrees with Kofron's (1979) earliest observation of vitellogenesis of 2 April for a Louisiana population. Oviductal eggs were observed as early as 31 May while other females were still vitellogenic (Fig. 12A), thus ovulation probably occurs in late May and early June. This ovulation date is consistent with estimates by Betz (1963) for a Missouri population. However, if gestation is approximately 3 months (Betz 1963), the early birth date observed in this study (Table 7) would place ovulation at around the middle third of April. Conversely, the ovarian cycle, or at least vitellogenesis, appears aseasonal in Veracruz (Aldridge et al., 1995). It appears, therefore, that Willow Lake female watersnakes have seasonal reproductive cycles typical of temperate snake populations as well as prenuptial vitellogenesis typical of viviparous colubrids (Seigel and Ford, 1987).

The male testes exhibited hypertrophy in early August which continued through much of the fall (Fig. 12B). This suggests that spermatogenesis was postnuptial for Willow Lake males which is typical of most colubrids (Seigel and Ford, 1987). Although the population from Veracruz was classified as having a prenuptial spermatogenic cycle (Aldridge et al. 1995; Keck, 2004), there appears to be more similarities to a postnuptial

cycle for that population. Spermatogenesis did begin and end one month later in Veracruz than for this population, but was completed at least two months before the first female was detected with sperm in oviducts of females (Aldridge et al. 1995). Therefore, there must be a period of sperm storage in the ductus deferens before mating; accordingly, reproductive behavior and androgen production are dissociated (Seigel and Ford, 1987). The two specimens (#76 and #106) in this study displaying unusually high mean testicular masses in spring (Fig. 12B) both had an anomalous growth in one testis. The remainder of the respective testicular tissue was quiescent.

Information on female and litter characteristics has been reported from various localities throughout the geographic range of *N. rhombifer* (Keck, 2004). Most are anecdotal observations (e.g., Tucker and Camerer, 1994; Judd and Bray, 1996) whereas others involved more detailed reproductive studies (e.g., Plummer, 1992; Aldridge et al. 1995). With the exception of the early birth date reported here (Table 7) the remainder of dates were within the period expected for north-temperate populations (Seigel and Ford, 1987) and other *Nerodia* (Gibbons and Dorcas, 2004). The exceptional birth date was on 19 July, two days earlier than the earliest reported date of 21 July (Judd and Bray, 1996). Interestingly, births from the litter were spread out over three days. Thirteen were born on 19 July, another on 20 July, and three more on 21 July, of which one was a full-formed stillborn.

Sex ratios for the three litters in this study were highly variable (Table 7), but overall primary sex ratio was not different from 1:1. Such observations appear to be typical for most snake populations (Parker and Plummer, 1987) and for this species (Plummer, 1992). Neonate lengths and masses (Table 7) were within the limits reviewed

by Keck (2004: Table 14, p. 167) for other *N. rhombifer* populations. The mean neonate length for all three litters combined was very similar to one litter also reported from Hidalgo County (22.8 cm: Judd and Bray, 1996), but there appears to be as much variability in the neonate SVLs and masses here as that seen throughout the distribution of *N. rhombifer* (Keck, 2004: Table 14). This variation may be due to maternal size since at a given SVL, heavier females had larger neonates (Plummer, 1992). Although all snake species do not express this type of phenotypic variability in offspring, those that do suggest the influence of governing factors such as genetics, maternal allocation, and environmental effects on the female and the developing embryos (Shine, 2003).

Maternal size was positively correlated with litter size and explained 52% of the variation in this trait for Hidalgo County *N. rhombifer* (regression:  $litter\ size = -30.7 + 0.503SVL$ ,  $N = 17$ ,  $R^2 = 0.520$ ,  $P = 0.001$ ). Of general consideration, this relationship was significant in more than three quarters of the snake populations reviewed by Seigel and Ford (1987), signifying relevance in both practical and theoretical matters (e.g., controlling for maternal size when comparing litter sizes). It appears that other populations of *N. rhombifer* also follow this trend (Fig. 13; Arkansas = 73%: Plummer, 1992; Veracruz = 40%: Aldridge et al., 1995; east central Texas = 63%: Keck, 2004). The unexplained variance in litter size by SVL suggests that genetic or environmental factors may be important determinants of fecundity (Seigel and Ford, 1987).

The significant differences in average litter size found among *N. rhombifer* populations after correcting for maternal SVL did not appear to be clinal (Fig. 14) and are likely confounded by the occurrence of plastic phenotypic responses to proximate factors rather than optimized traits associated with adaptations to dissimilar long-term and



prevailing environmental conditions (Seigel and Ford, 1991). For example, litter size may vary annually within the same population (Seigel and Fitch, 1985). Thus litter sizes in *N. rhombifer* may not be tightly constrained by genetic makeup of a population, but instead molded within certain genetic limitations by immediately encountered conditions such as food availability (Ford and Seigel, 1989). More detailed field and common garden studies are needed to elucidate the nature of the variation in litter size, and more generally maternal investment, as they relate to optimized reproductive strategies among populations of this widely distributed species. Shine (2003) reviews some of the factors associated with reproductive strategies that may be responsible for the observed differences in litter size among *N. rhombifer* populations. Shine's (2003) review should be useful in designing future studies that evaluate geographic variation in reproduction. Among these factors are female body condition, energy allocation, food availability, offspring size and quality, and thermal preference during gestation.

*Sexual Size Dimorphism.*—The minimum and maximum sizes for Willow Lake *N. rhombifer* (Table 9) were within the limits reviewed by Keck (2004). Female-biased sexual size dimorphism (SSD) for body size (SVL) was observed as in other populations of North American watersnakes including diamondbacks (Gibbons and Dorcas, 2004; Keck, 2004; Winne et al., 2005). The ranges for SVL for the top 25% of the male and female subsamples did not show overlap (maximum male = 93.5 cm, minimum female = 97.3 cm). This dimorphism was mirrored by the differential size at maturation in this population as the smallest mature male was 31% smaller than the smallest reproductive female (Table 6). Snake populations in which females grow to larger sizes than males

make up about 67% of the populations studied (Shine, 1993). Female-biased SSD is associated with the absence of male-male combat (Shine, 1994), reduced fecundity-dependent costs for males, and maximizing reproductive success in females by delaying maturity to increase clutch size for the first reproductive effort (Shine, 1993). The proximate mechanisms that are responsible for females attaining larger sizes include sexual bimaturation, reduced growth rates after maturation, lower survival rates in males, and faster female growth (Shine 1993). Indeed, each of these mechanisms was observed in *N. rhombifer* from south Texas.

Willow Lake *N. rhombifer* expressed male-biased SSD for TL. Longer tails appear to be typical of other North American watersnakes (Semlitsch and Gibbons, 1982; Winne et al., 2005). According to Shine's (1993) review male-biased SSD for TL is also seen in many snake species and appears to have functional significance in housing the hemipenes and retractor muscles (King, 1989; Shine, 1993).

As with SVL, there was female-biased SSD for mass, however this was expressed as a difference in the rate at which mass was gained. This was indicated by the significant difference in slopes (scaling coefficients; Figs. 2 and 16). According to this analysis, the change in the rate at which females gained mass with size was greater than in males. While the analysis was confounded because gravid females were not separated in the analysis, it demonstrates that at least mature females exhibited a considerably increased allometric mass-length ratio. Since mass was used as a proxy for body form, this indicated that females, perhaps because of gravidity, had stouter bodies. Wider body forms for females are viewed as the product of fecundity selection as more space is available for offspring (Semlitsch and Gibbons, 1982; Shine, 1993). Whether or not non-

gravid female *N. rhombifer* are more robust in build than males is a question that cannot be answered with this data set. Although the data do not allow one to draw conclusions about body form without gravid females included, there was a qualitative intersexual body shape *gestalt* allowing for some accuracy in predicting sex before closer inspection. Similarly, other data sets for other *Nerodia* species have found that females are more massive than males but also failed to separate gravid from non-gravid females (Semlitsch and Gibbons, 1982; King et al., 1999). There appears to be evidence that females of some species are heavier than males regardless of reproductive condition (*Acrochordus arafurae*: Shine, 1986; *S. pygaea*: Winne et al., 2005) or age (*Acrochordus arafurae*: Shine, 1986; *Storeria dekayi* and *Thamnophis sirtalis*: King et al., 1999; *T. sirtalis*: Krause and Burghardt, 2007). For *S. pygaea* from South Carolina, Winne et al. (2005) found significant differences between females and males in size corrected body mass; both gravid females and non-gravid females were heavier than males at a given SVL.

Of the size dimensions studied for neonates from three litters, the grand means for SVL and mass were greater for females (Table 10), however after controlling for maternal (litter) influence (nested within sex and treated as random to make inferences about the population) neither SVL or mass were significantly different between males and females (Table 11). There was significant variation however among litters within sex indicating maternal or genetic influence on both SVL (Fig. 17) and mass. Indeed variation within and among litters has been observed in snakes and has been related to maternal condition, litter or clutch size, and genotypes (Plummer, 1992; Krause and Burghardt, 2007). Weatherhead et al. (1995) found that female neonate *N. sipedon* from eastern Ontario, Canada had significantly higher SVL and mass than neonate males.

Conversely, King et al. (1999) did not find a significant difference in body size for conspecific neonates from Ohio, although the SSD index used for this population favored female neonates in both SVL and mass. Interestingly a separate one-way ANCOVA (not shown) treating all neonates in this study as random variants, though not appropriate for the data set, approached significance ( $P = 0.060$ ) with females having greater masses. These consistencies in female-biased body size dimensions in *Nerodia*, while not significant, may indicate that the mechanisms regulating size differences are at work in the prenatal environment. It has been proposed that such differences may be due to differential maternal energy allocation (Krause and Burghardt, 2007), however data on first and second year postnatal growth on three separate litters of *Nerodia* showed that there were female-biased differences in the ratio of production to ingestion suggesting that females had higher dietary assimilation efficiencies or allocated more energy to growth (Scudder-Davis and Burghardt, 1996). These metabolic differences, if they exist, should be present during prenatal development.

*Growth.* —Despite some of the complications associated with fitting the growth data for *N. rhombifer* from Willow Lake to growth curves (e.g., using a combination of longitudinal and cross-sectional data, and highly variable time intervals in which growth increments were recorded; see Kaufmann, 1981, for discussion), all growth curves appear to provide one of the likely mechanisms for the observed female biased SSD for body length. Given some of the assumptions taken in constructing these models it is not surprising that the growth model that is commonly used to describe reptilian growth, the von Bertalanffy (e.g., Van Devender, 1978; Plummer, 1985; Brito and Rebelo, 2003;

Stanford and King, 2004), was the least useful in explaining the average rate changes in growth with size in these samples. Perhaps this is a consequence of using growth increments with variable and wide-ranging time intervals, observed not just through days but across seasons and years. Because reptilian growth is known to fluctuate seasonally (Van Devender, 1978; Andrews, 1982) and using too short or too long a time interval for a growth measurement can introduce biases (Andrews, 1982), the limitations of the data sets used here (i.e., low capture rates within any given season) make estimating the effects of such biases extremely difficult. Furthermore, the regression models upon visual inspection showed problems with heteroscedasticity (Fig. 18) and 21% of male growth rates and 28% of female growth rates were repeat measures making the variants not entirely independent. Thus, the data should be interpreted with caution.

Considering these flaws, the results represent the first attempt to provide a comprehensive quantitative description of growth for *N. rhombifer* from a field population. Assuming that all biases affecting the estimates of growth rates are equal between the male and female data sets some rough conclusions can be drawn. Females had a tendency to grow at faster rates (Figs 18 and 19) although this difference was not statistically significant. This could in part explain SSD seen in adults. Using the minimum ages at maturity for each sex (male: 518 mm, female: 755 mm) and the respective power growth curves (Fig. 19), males mature at about 1.5 yr and females at 2.5 yr (after converting the age function in days to years). Because growth rates slow when reptiles reach maturity (Andrews, 1982), the delay in maturity of females by one year provides another mechanism for the observed SSD. The age at maturity estimates in this

study also agree with those Betz (1963) for females (2.2 yr) and M. Keck (Keck, 2004) for males (1.2 yr) and for females (2.2 yr).

Keck (2004) noted that the only data available for growth of *N. rhombifer* in the field was from an Oklahoma study by Preston (1970). The following account of these data is based on Keck (2004). The sample sizes for the age groups were small and measured during the active season (from April-October). For individuals  $\leq 1$  yr in age, males ( $N = 2$ ) grew at about 0.32% of their SVL per day and females ( $N = 4$ ) grew at 0.22%. For individuals between 1 and 2 yr in age, males ( $N = 4$ ) grew at 0.09% and females ( $N = 1$ ) 0.17%. Males greater than 2 yr in age ( $N = 4$ ) grew at 0.04% and females ( $N = 1$ ) grew at 0.01%. Clearly, the sample sizes are too small to determine if the Oklahoma population exhibited sexual dimorphism for growth rate. In comparison with the specific growth rate estimates from this study (Table 13), the percent growth estimates from the Oklahoma population for the first age group correspond to a 39 cm male at about 1.1 yr in age and a 49 cm female at about 1.2 yr in age. For the second age group, the estimates correspond to a 57 cm male at about 1.7 yr in age and a 53 cm female at about 1.5 yr in age. In the age group described as  $> 2$  yr, the estimates correspond to a 73 cm male at about 2.9 yr in age and a 120 cm female at about 8.5 yr in age.

*Nerodia rhombifer* from Willow Lake may exhibit sexual dimorphism in growth rate. However, the relative importance of the proximate mechanisms that lead to the observed SSD require more field studies. Detailed demographic and growth data could provide insight on how selective forces shape the life history characteristics for this species. Field growth rates are virtually unknown for all *Nerodia* species and few

detailed demographic studies are available (Gibbons and Dorcas, 2004). Although, data on growth rates for *N. sipedon* showed that females grew at significantly greater rates than males (King, 1986), and females of *N. rhombifer* grew faster than their siblings in a laboratory setting (Scudder-Davis, 1996) suggesting that differential growth rates may play a significant role in determining adult sizes in *Nerodia*.

*Lipids.*—The positive correlations between fatbody mass (FBM) and size for both sexes (Figs. 20 and 21) were expected as larger snakes have a greater coelomic volume (Seigel and Ford, 1987). Larger snakes also may have a greater variety of food items available to them because of reduced limitations of gape size (Arnold, 1993; King 2002).

Consequently, larger snakes may take larger prey (Plummer and Goy, 1984), and may have greater foraging success (Lind and Welsh, Jr., 1994).

There was little size overlap between males and females (Figs. 20 and 21) making an intersexual comparison of FBM difficult. However, the FBM-SVL and FBM-BM regression lines suggest that per unit SVL and per unit mass, males stored more lipids in fatbodies than did females where size did overlap (at 75.5 cm and 400 grams). If these differences were significant, male and female *N. rhombifer* from south Texas might compartmentalize lipids differently.

Aldridge et al. (2003) did not find a significant difference between the regression lines of FBM and SVL for *N. rhombifer werleri* from Veracruz, Mexico. This comparison may be confounded by dimorphism for body form where female *N. rhombifer* appear to be wider than males, as seen in a number of species (Shine, 1993). Because of this attribute among *N. rhombifer* populations, FBM by BM comparisons may

be more instructive biologically. For example, male *Natrix maura* in the Ebro Delta of northeastern Spain had heavier carcasses after controlling for SVL than did females even though the absolute amount of lipids stored in this compartment, also controlled for SVL, were not different (Santos and Llorente, 2004). Conversely, female *N. maura* had larger livers and stored more lipids in this organ than did males (Santos and Lorente, 2004). Numerous studies also have generally noted an inverse correlation between fatbody size and vitellogenesis (Seigel and Ford, 1987; Blem and Blem, 1990; Aldridge and Bufalino, 2003). Thus, in reproductively active females, vitellogenic follicles, oviductal eggs and embryos would contain a significant portion of overall lipids in females.

Indeed these observations reflect the different ecological roles of males and females. Females invest much energy in the production of offspring, while males may invest significantly more through active mate searching and courtship. Although the regression models from Figures 20 and 21 do not reflect these roles, it is likely that more matter and energy pass through females than males during a calendar year. The apparent difficulty in observing this from snapshots of FBM is due to differential compartmentalization and rates of utilization of body lipids between sexes.

Despite the obstacles associated with using fatbodies to describe the dynamics of lipid reserves for different aspects of snake life history, variation in FBM may be useful in tracking changes in overall lipid reserves since fatbodies can be the main component of (Santos and Llorente, 2004), and can be highly correlated to, total body lipids (Blem, 1997). Observations of changes in FBI (FBM corrected for body size) in male *N. rhombifer* from south Texas suggest that males go through cycles of fat storage and mobilization. The lowest FBI values for males were in spring and began to increase in



early summer (Figs. 23 and 24). A similar pattern was observed for male *N. rhombifer* from Veracruz (Aldridge et al. 2003). The shift in energy balance coincides with changes in activity (Fig. 6C). Peak activity for males was observed in May, the same month in which the lowest FBI values were recorded. The initial increase to peak activity in May is likely associated with mate searching as suggested for males of other species (e.g. *Coluber viridiflavus*: Bonnet and Naulleau, 1996). However, the increase in activity was sustained through July. If this is beyond peak mating activity, then there must be a reduction in feeding while males are searching for and courting females.

Circumstantial evidence suggests not only that male *N. rhombifer* from south Texas stop feeding during a short period, but that this aphagia is endogenous as seen in *Thamnophis sirtalis parietalis* (O'Donnell et al., 2004). The evidence includes the concomitant peak activity with drop in FBI in May for males in this population, reported dates for mating in the field (6 April to 29 May: Keck, 2004; Zamora and Valadez, 2007), estimated gestation period (3 months: Betz, 1963) and peak birth dates (14 of 25 births from 20 August to 10 September: Keck, 2004), and an apparent lack of interest by several males in both feeding and a potential predator while courting a female (Zamora and Valadez, 2007).

Unlike males, females did not exhibit significant variation in FBI among months. This was similar for female *N. rhombifer werleri* from Veracruz, Mexico (Aldridge et al., 2003). Although, Aldridge and Bufalino (2003) suggest that other *Nerodia* may display a decrease in the mass of fatbodies during vitellogenesis as observed for females of other species (Seigel and Ford, 1987). Such losses may have been regained during pregnancy (Aldridge and Bufalino, 2003). However, any seasonal differences in fatbodies among

female *Nerodia* may be less dramatic than in other snake populations (e.g., *Cortals atrox*: Tinkle, 1962; *Agkistrodon piscivorus*: Blem, 1997).

Because the BM used to calculate FBI in this study included the mass—depending on the reproductive state of the female—of quiescent ovaries, vitellogenic follicles, oviductal eggs and embryos, one would expect FBI to be relatively lower in reproductively active females even when the mass of fatbodies remains relatively stable because vitellogenic follicles and developing embryos would increase the BM (the denominator used to calculate FBI) relative to FBM. The FBI values reported here for females in all categories, both reproductive and non-reproductive, appear to be similar (Figs. 21B and 23B). Although no detailed feeding frequency analyses were performed here because of potential biases from sampling actively foraging snakes (see Preston, 1970; Aldridge et al., 2003), these data provide indirect evidence that female *N. rhombifer* from south Texas continue to feed at a rate at least equal to that which would replenish lipid reserves used during vitellogenesis. Conversely, several species of snakes have been observed to reduce food intake during pregnancy (Shine, 1980b). This *modus operandi*, whether adaptive or artifact, would require energy storage prior to the onset of vitellogenesis that could then be used at a later time to support the production of offspring, a tactic referred to as “capital” breeding (Bonnet et al., 1998). A strict capital breeder should display a strong cycling of lipid reserves. The alternative is referred to as “income” breeding in which recently acquired nutrients are used (Bonnet et al. 1998). There are numerous examples in which snakes may not only supplement vitellogenesis by foraging during this time but continue to feed through oviposition, or parturition (Berry and Lim, 1967; Aldridge and Bufalino, 2003;

Winne et al., 2006). The lack of evidence for cycling of fatbody lipids in this study implies that female *N. rhombifer* from south Texas exhibit a significant degree of income breeding.

## CHAPTER V

### CONCLUSIONS

Capture rates for Willow Lake *Nerodia rhombifer* (about one snake for every 24 trap-days) were low as in other snake studies. Such low capture rates result in absolute abundance estimates with very broad confidence limits. Increasing trapping effort over several days per trapping period and the use of drift fences might improve capture rates and narrow confidence limits for abundance estimates. Despite a lack of precision in the abundance estimates reported here for Willow Lake *N. rhombifer*, the average density for all sampling periods in which estimates were calculated, 6.6 snakes/ha (Table 4), is still greater than the median value for 57 populations reviewed by Parker and Plummer (1987). The relatively high density of this population is likely supported by relatively high primary productivity typical of wetlands that occur along river flood plains. The standing crops calculated from the density values reported here indicate that *N. rhombifer* is a significant component of the Willow Lake ecosystem. The densities on which the biomass estimates are based are the first true density estimates reported anywhere within the range of *N. rhombifer*.

The relative abundance estimates used to measure activity in this study indicated that Willow Lake *N. rhombifer* increased activity from May through September. This observed active season was sustained a month longer than for populations in

Louisiana and northeastern Texas (Fig. 25). Activity was reduced significantly from October through January of the following calendar year, but activity slowly increased from February to April. This overall activity pattern appears to be similar to other subtropical snake populations from Florida (Dalrymple et al., 1991). Adult and juvenile subpopulations of Willow Lake *N. rhombifer* differed in activity patterns, however all displayed two peaks in activity. When the data from the subpopulations are combined, the variation among the subpopulation activity patterns resulted in an overall decrease in activity during July (Figs. 4 and 25). The differences in activity patterns among subpopulations are probably due to differences in the types of activities associated with life history patterns that are shaped by selective forces that dictate fitness for individuals within a given cohort.

Adult males displayed a strong bimodal activity pattern with an initial peak activity in May and another in September. An approximate 66% drop in adult male activity was observed in August resulting in the two activity peaks (Fig. 6C). Although the activity pattern for adult females was not as strongly bimodal as adult males, females displayed peaks in activity in June and September with an approximate 24% drop in activity in July (Fig. 6B). Juveniles also displayed a strong bimodal activity pattern similar to adult males, however a dip in activity was observed from June to July (Fig. 6A). The activity pattern of juveniles is likely confounded by births in summer and early fall and by second year juveniles moving to into adult cohorts. Interestingly, although the overall activity pattern for the Willow Lake population appears slightly bimodal, analyses of the activity patterns of the subpopulations indicate that the small dip in activity

observed in July for the overall population (Fig. 4B) may be due to more significant trends occurring within the subpopulations.

Survivorship curves estimated from the age structure of Willow Lake *N. rhombifer* showed both high mortality rates and low longevity (Fig. 26). Further, data on reproduction and growth indicated that Willow Lake *N. rhombifer* have short generation times (2.5 yr), have high fecundity (average litter size, 15.4), and reproduce annually. These demographic characteristics displayed by Willow Lake *N. rhombifer* appear to be typical of other early maturing Colubridae (Parker and Plummer, 1987).

Overall primary and secondary sex ratios did not differ significantly from 1:1. In seasonal comparisons of sex ratios, a significantly female-biased sex ratio (1.8:1.0) was observed only in August. This difference was probably due to changes in activity patterns between females and males.

Reproduction in *N. rhombifer* in Hidalgo County appears to be seasonal. Mating is known to occur as early as April (Meade, 1934; Zamora and Valadez, 2007). In females, vitellogenic follicles were observed as early as 27 May, however vitellogenesis probably begins in early to mid-April. Ovulation likely occurs in late May or early June. The last reproductive female was observed on 30 September with vascular spots in the uterus indicating recent parturition. In males, testes were enlarged from early August through fall. Thus, spermatogenesis was postnuptial which is typical of most colubrids (Seigel and Ford, 1987).

An exceptionally early birth date for *N. rhombifer* was recorded in Hidalgo County on 19 July, but the general progression of female reproductive structures such as vitellogenic follicles and developing embryos, and two other birth dates were within the

range reported for other *N. rhombifer* populations (Keck, 2004). Litter size for Hidalgo County *N. rhombifer* was positively correlated to maternal SVL as seen in many other snake populations and was significantly lower than populations from Arkansas and Veracruz, but not east-central Texas (Fig. 14). Thus, litter size variation in *N. rhombifer* populations does not appear to be clinal. It is likely that litter size is a phenotypically plastic trait and its expression is dependent upon immediately encountered environmental conditions such as food availability (Ford and Seigel, 1989; Seigel and Ford, 1991). Consequently, variation in litter sizes among *N. rhombifer* populations can be better understood only with consideration of the proximate factors that influence litter sizes.

*Nerodia rhombifer* in southernmost Texas are sexually dimorphic for size with females being larger in SVL and mass than males. The largest female captured was 120.0 cm SVL and the largest male captured was 93.5 cm SVL. The rate at which mass changed with SVL was greater for females (Figs. 2 and 16) indicating that females were wider in body form. The female biased sexual size dimorphism is typical of North American watersnakes (Gibbons and Dorcas, 2004; Keck, 2004; Winne et al., 2005) and is thought to occur in a wider range of snake taxa, in part, as a consequence of fecundity selection (Shine, 1993). Conversely, males had longer tails proportionately than did females. The larger tails in males function to house the hemipenes and retractor muscles (King, 1989; Shine, 1993). The male-biased sexual dimorphism for tail length was already present at birth. However, no differences were detected between male and female neonates both for SVL and for mass. Maternal females appeared to have an influence on the size of neonates as larger females gave birth to larger young (Fig. 17).

Female *N. rhombifer* in Willow Lake had slightly higher average growth rates at a given SVL than males. Although not significant, this difference in growth may be real, but problems with precision in estimating female and male growth curves in this study made resolving this issue difficult. Indeed, other *Nerodia* have been shown to exhibit female biased growth rates (King, 1986; Scudder-Davis, 1996). Furthermore, power analyses in general demonstrate that given a large enough sample size a statistical significance will always be found between two populations (Nakagawa and Cuthill, 2007). The question remains as to whether such differences are biologically significant or not. Because growth curves derived from cross-sectional data should provide a good approximation of average growth rates for a population at a given size (Marvin, 2001), assuming that the negative and positive biases that contributed to decreased precision in this analysis had similar influences on both sexes, the average differences in growth rates at a given size (Table 13) should be biologically significant. Such differences in growth rates could, in part, along with differential mortality rates and sexual bimaturism, explain the observed female-biased sexual size dimorphism for SVL in this population.

The precision in the growth curves generated from growth increments (calculated as a change in length per unit of time) depends on precision of the growth increments themselves. Precision could be improved by increasing trapping effort as described above. The increased effort should increase the number of snakes recaptured within regular time intervals and within a specific time period. Regular time intervals are necessary to reduce biases associated with the calculation of rates. If a time interval used to calculate a growth increment is too long, it causes negative bias; too short, positive bias. Growth rates in snakes also are known to vary throughout the year (Andrews, 1982)



emphasizing the need to use a specified time period (e.g., a calendar year, or a season) in which growth increments will be observed. Furthermore, a squeeze box (Quinn and Jones, 1974) could be used to reduce the error associated with stretching snakes to obtain lengths. Accordingly, given an adequate but constant time period in which to estimate individual growth increments along with the use of a squeeze box, negative growth rates could virtually be eliminated and precision improved.

Female *N rhombifer* in southernmost Texas did not show evidence for lipid cycling from fatbody mass data and may then be categorized as income breeders. Indeed, anecdotal observations suggest that vitellogenic and gravid females continue to forage in the field even as their increased mass may make them more vulnerable to predation. In one such instance, while trapping snakes in Willow Lake, two large gravid female *N. rhombifer* attempted to ingest the same large *Siren intermedia* while all three were captured in the same trap. Further, except for the relatively small dip in activity in July (Fig. 6B), females remained highly active and presumably feeding within the trapping grids at Willow Lake during the time in which they are reproductively active (April to September). Males appeared to cycle lipids as fatbody masses displayed significant declines in early spring. This coincides with the time in which mating activity has been observed. Because this species is largely restricted to water, opportunities to feed on fish should have been available. Therefore, the reduction in fatbody mass during this time period suggests either that more energy was used than was ingested, or that males became anorexic, or both. Lipid reserves in males are apparently quickly regained after the mating season (Fig. 23A).

TABLE 1. Summary of trapping effort for *Nerodia rhombifer* from Willow Lake at Santa Ana National Wildlife Refuge. Each bi-weekly trapping period encompassed two consecutive days. Fifty-one traps were set each day of the trapping period. Effort for the entire study was 6222 trap-days. Number of periods per month is in parentheses. Total number of periods for each month (years combined) and each year are also presented. Because capture rates were low, capture data were pooled by month making a total of 31 sampling periods.

Month	Trapping Dates				Total Periods
	1995	1996	1997	1998	
January			9, 10, 23, 24 (2)		2
February		21, 22 (1)	6, 7, 20, 21 (2)		3
March		6, 7, 20, 21 (2)	6, 7, 20, 21 (2)	27, 28 (1)	5
April		3, 4, 17, 18 (2)	3, 4, 17, 18 (2)	10, 11, 24, 25 (2)	6
May		1, 2, 15, 16, 30, 31 (3)	1, 2, 15, 16, 29, 30 (3)	8, 9, 20, 21 (2)	8
June		12, 13, 26, 27 (2)	12, 13, 26, 27 (2)	3, 4, 17, 18 (2)	6
July		10, 11, 24, 25 (2)	10, 11, 26, 27 (2)	1, 2, 15, 16, 29, 30 (3)	7
August	30, 31 (1)	7, 8, 21, 22 (2)	9, 10 (1)	12, 13, 26, 27 (2)	6
September	13, 14 (1)	4, 5, 19, 20 (2)		9, 10, 24, 25 (2)	5
October		3, 4, 17, 18, 31 (2.5)		8, 9, 22, 23 (2)	4.5
November		1, 14, 15, 28, 29 (2.5)		5, 6, 19, 20 (2)	4.5
December		12, 13, 26, 27 (2)		3, 4, 17, 18 (2)	4
Total Periods	2	23	16	20	61

TABLE 2. Equations for the growth models tested for fit to growth increments collected on *Nerodia rhombifer* from Willow Lake at Santa Ana National Wildlife Refuge. The first von Bertalanffy equation follows Van Devender (1978); and the second Von Bertalanffy equation, and the logistic, Gompertz, and power equations follow Kaufmann (1981). The integrated equations on the left are the more commonly used forms and show size ( $S$ ) as a function of time ( $t$ ). The differential equations show the relationship between the measure of growth rate ( $GR$  or  $G$ ) and size.  $GR$  is the growth rate and  $G$  is the specific growth rate as defined in the text. The relationship is linear when  $S$  is properly transformed.  $S_\infty$  is the asymptote of the integrated equations for determinate growth models. The relationship between  $S_\infty$ ,  $a$ , and  $b$  is shown in the right hand column. The parameter  $t_o$  is the constant of integration. All equations follow Kaufmann's (1981) notation.

Integrated Equation	Differential Equation	Relation of the Parameters
Von Bertalanffy $SVL = SVL_\infty + [\exp a(t - t_o)] a^{-1}$	$GR = -aSVL + b$	$SVL_\infty = -\frac{b}{a}$
Von Bertalanffy $S = S_\infty[1 - \exp - b(t + t_o)]$	$G = a\frac{1}{S} - b$	$\frac{1}{S_\infty} = -\frac{b}{a}$
Logistic $S = S_\infty[1 + \exp - b(t + t_o)]^{-1}$	$G = -aS + b$	$S_\infty = -\frac{b}{a}$
Gompertz $S = S_\infty \exp[-\exp - a(t + t_o)]$	$G = -a \ln S + b$	$\ln S_\infty = -\frac{b}{a}$
Power $S = [ab(t + t_o)]^{1/a}$	$\ln G = -a \ln S + \ln b$	—

TABLE 3. Summary of capture rates for *Nerodia rhombifer* over 31 monthly trapping periods at Santa Ana National Wildlife Refuge. Individuals recaptured within the same month were not counted. Individuals recaptured in subsequent months were counted as recaptures for absolute abundance estimates and simply as captures for relative abundance indexes. Capture and recapture rates are based on 31 trapping periods. Percent recaptures were calculated from the ratios of recapture rate to total capture rate for each grouping. Juveniles were defined as any individual < 51.8 cm, the size of the smallest mature male in this study. Effort for trapping periods ranged from 102-306 trap-days, most were 204 trap-days.

	All	Cohort		
		Juvenile	Adult Female	Adult Male
No. of individuals <sup>a</sup>	154 <sup>a</sup>	38	69	58
No. of captures	232	45	103	84
No. of individuals captured 1×	100	32	45	39
No. of individuals recaptured 1×	36	5	16	12
No. of individuals recaptured 2×	12	1	6	7
No. of individuals recaptured 3×	6	0	2	0
Capture rate (snakes/period)	7.48	1.45	3.32	2.71
Recapture rate (snakes/period)	2.52	0.226	1.10	1.00
Percent recapture	33.7 %	15.6 %	33.1 %	36.9 %

<sup>a</sup>Lack of correct summation of cohorts is due to some juveniles that were captured earlier during field work and then captured again later as adults.

TABLE 4. Comparison of population sizes generated using three different methods of estimation for mark-recapture data taken from a population of *Nerodia rhombifer* at Santa Ana National Wildlife Refuge. Numbers were calculated by combining data from Grids 1 and 2, a total area equal to 0.32 ha. Densities are based on Jolly-Seber estimates and a study area of 7.2 ha. Biomass is calculated from the mass structure, mean mass = 396.3 g.  $N$  = population size estimate, C.L. = confidence limits, MNA = minimum number known to be alive.

Month	Schnabel		Jolly-Seber		MNA	Density (ha <sup>-1</sup> )	Biomass (kg/ha)
	$N$	95 % C.L.	$N$	95 % C.L.			
Aug-95	-	-	-	-	6	-	-
Sep-95	85.0	(16.0 - 1666.7)	41.4	(17.5 - 415.2)	18	5.8	2.3
			$\bar{N} = 41.4$	(17.5 - 415.2)			
Feb-96	106.0	(19.9 - 2078.4)	20.0	(2.5 - 604.0)	6	2.8	1.1
Mar-96	150.0	(28.2 - 2941.2)	45.0	(5.4 - 1406.5)	7	6.3	2.5
Apr-96	147.0	(44.0 - 828.2)	36.2	(10.5 - 332.7)	10	5.0	2.0
May-96	189.5	(79.0 - 554.9)	54.1	(23.6 - 263.9)	20	7.5	3.0
Jun-96	176.5	(82.6 - 405.3)	66.0	(22.2 - 399.4)	18	9.2	3.6
Jul-96	201.2	(108.0 - 406.1)	85.0	(37.4 - 342.3)	26	11.8	4.7
Aug-96	188.7	(119.1 - 349.4)	115.7	(51.3 - 438.9)	30	16.1	6.4
Sep-96	169.4	(114.4 - 261.1)	75.8	(32.9 - 311.3)	24	10.5	4.2
Oct-96	168.8	(116.9 - 271.6)	37.5	(6.8 - 584.1)	14	5.2	2.1
Nov-96	175.4	(121.4 - 282.2)	108.0	(11.9 - 3286.8)	14	15.0	5.9
Dec-96	175.4	(121.4 - 282.2)	12.0	(1.2 - 357.5)	12	1.7	0.7
			$\bar{N} = 59.6$	(18.70 - 757.04)			
Jan-97	178.8	(123.8 - 287.6)	48.0	(5.4 - 1439.5)	13	6.7	2.6
Feb-97	171.3	(118.3 - 265.7)	32.0	(5.9 - 496.2)	12	4.4	1.8

TABLE 4. Continued.

Month	Schnabel		Jolly-Seber		MNA	Density (ha <sup>-1</sup> )	Biomass (kg/ha)
	<i>N</i>	95 % C.L.	<i>N</i>	95 % C.L.			
Mar-97	174.1	(123.2 - 266.6)	20.0	(6.2 - 149.1)	12	2.8	1.1
Apr-97	176.0	(125.6 - 255.5)	61.3	(21.8 - 352)	17	8.5	3.4
May-97	204.2	(149.9 - 302.0)	76.0	(35.0 - 300.8)	25	10.6	4.2
Jun-97	212.2	(160.1 - 288.1)	45.6	(26.3 - 134.2)	24	6.3	2.5
Jul-97	217.0	(167.0 - 288.0)	64.0	(26.2 - 320.2)	20	8.9	3.5
Aug-97	221.9	(170.8 - 294.5)	63.0	(7.3 - 1944.4)	9	8.8	3.5
			$\bar{N} = 51.2$	(16.8 - 642.0)			
Mar-98	229.7	(177.9 - 324.0)	24.6	(8.5 - 170.0)	11	3.4	1.4
Apr-98	232.6	(180.7 - 326.6)	26.0	(7.2 - 223.8)	12	3.6	1.4
May-98	237.7	(186.9 - 326.4)	38.0	(19.1 - 141.9)	18	5.3	2.1
Jun-98	246.5	(195.3 - 334.1)	30.2	(15.5 - 111.2)	16	4.2	1.7
Jul-98	250.0	(198.8 - 336.7)	25.6	(9.8 - 137.0)	14	3.6	1.4
Aug-98	241.8	(194.4 - 319.8)	38.3	(13.9 - 235.5)	14	5.3	2.1
Sep-98	238.7	(193.0 - 312.8)	26.4	(6.9 - 346.1)	8	3.7	1.5
Oct-98	236.3	(191.6 - 308.3)	5.0	(2.0 - 63.9)	3	0.7	0.3
Nov-98	237.1	(192.5 - 308.5)	-	-	-	-	-
			$\bar{N} = 26.8$	(10.4 - 178.7)			
Average	194.4	(131.7 - 533.5)	47.6	(15.3 - 245.4)	14.5	6.6	2.60

TABLE 5. Mean snout-vent length (SVL) and mass for the sample used to construct size and age structures for *Nerodia rhombifer* from Willow Lake at Santa Ana National Wildlife Refuge. The sample includes 175 size records for 154 individuals. Records of individuals recaptured within the same calendar year were excluded from the analysis. Records of individuals recaptured in other years were included. Thus, 21 size records included in these summaries are from inter-year recaptures. *N* = sample size, SE = standard error.

	<i>N</i>	SVL (cm)		Mass (g)	
		Mean (SE)	Range	Mean (SE)	Range
Juvenile	39	37.72 (1.49)	20.7 – 51.0	49.678 (4.873)	7.40 – 108.80
Female	73	84.86 (2.39)	51.9 – 120.0	690.674 (59.570)	106.50 – 1880.90
Male	63	70.93 (1.30)	52.8 – 94.9	269.783 (13.632)	68.00 – 508.40
All	175	69.34 (1.78)	20.7 – 120.0	396.302 (32.129)	7.40 – 1880.90

TABLE 6. Mean SVL and mass for specimens collected from irrigation canals in Hidalgo County, Texas. (A) Characteristics for all females and males examined for reproduction. (B) Characteristics for reproductive females and mature males only. F = female, M = male, *N* = sample size, SVL = snout-vent length, SE = standard error.

	Sex	SVL (cm)			Mass (g)		
		<i>N</i>	Mean (SE)	Range	<i>N</i>	Mean (SE)	Range
A	F	71	80.12 (1.70)	50.60 – 112.70	71	553.2 (35.9)	111.0 – 1564.5
	M	54	64.16 (0.99)	48.40 – 78.80	53 <sup>a</sup>	237.6 (11.7)	68.3 – 481.4
B	F	21	90.14 (2.22)	75.50 – 112.70	21	812.4 (56.5)	494.0 – 1564.5
	M	53	64.46 (0.959)	51.80 – 78.80	52 <sup>a</sup>	240.9 (11.4)	86.1 – 481.4

<sup>a</sup> Reduced sample size of male sample due to severe freeze dehydration of one of the specimens.



TABLE 7. Female and litter characteristics for *Nerodia rhombifer* collected from irrigation canals in Hidalgo County, Texas. SVL = snout-vent length, SE = standard error, F = female, M = male, U = sex undetermined.

Female	SVL (cm)	Mass (g)	Litter Size	Neonate		Sex Ratio	Birth Date
				SVL (cm) Mean (SE)	Mass (g) Mean (SE)		
1	83.0	553.4	14	19.81 (0.37) <sup>a</sup>	6.50 (0.41) <sup>a</sup>	5F:8M:1U	9/12/1997
2	89.8	660.0	17	24.05 (0.15)	10.91 (0.12)	12F:5M	7/19-7/21/2003
3	85.0	733.3	12	23.21 (0.16)	9.38 (0.11)	3F:9M	8/21/2003
Mean (SE)	85.7 (1.76)	648.9 (52.2)	14.3 (1.45)	22.4 (0.32)	9.05 (0.32)	—	—
Total/Range	—	—	—	—	—	20F:22M:1U	7/19-9/12

<sup>a</sup> Two births were stillborn and two were stillborn and underdeveloped. All four stillborns were smaller than the individuals born live.

TABLE 8. Female and litter size characteristics for four populations from subtropical, temperate and tropical regions. The results of the correlation analyses between litter size and snout-vent length (SVL) also are reported.  $N$  = sample size, SE = standard error,  $r$  = correlation coefficient,  $P$  = probability that null hypothesis is true.

Location	$N$	Female SVL (cm)		Litter Size		$r$	$P$	Data Source
		Mean (SE)	Range	Mean (SE)	Range			
Hidalgo Co, TX	17	91.66 (2.912)	75.5-115.0	15.4 (2.03)	4-39	0.721	0.001	This study
Lonoke Co, AK	21	90.82 (2.114)	78.5-109.1	23.1 (2.10)	12-48	0.857	< 0.001	Plummer (1992)
Freestone Co, TX	13	87.96 (2.010)	74.5-98.5	16.1 (2.29)	7-35	0.791	0.001	M. Keck (Unpublished Data)
Veracruz, Mex	14	84.54 (2.441)	74.0-102.6	17.1 (2.24)	8-35	0.633	0.015	Aldridge et al. (1995)

TABLE 9. Size summaries for *Nerodia rhombifer* from Willow Lake, Santa Ana National Wildlife Refuge. For individuals captured more than once, only the first record of capture was used in the analysis. Individuals with incomplete size records or that were not sexed were not included in the analysis. F = female, M = male, *N* = sample size, SVL = snout-vent length, TL = tail length, SE = standard error.

Sex	<i>N</i>	SVL (cm)		TL (cm)		Mass (g)	
		Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range
F	76	75.96 (2.95)	22.3-120.0	17.64 (0.75)	4.3 – 37.4	560.7 (60.6)	10.5 – 1880.9
M	62	67.32 (1.58)	33.6-93.5	18.90 (0.62)	8.2 – 28.6	237.0 (14.7)	27.1 – 460.1

TABLE 10. Summary of neonate sizes born to three female *Nerodia rhombifer* collected in Hidalgo County, Texas. F = female, M = male, U = sex undetermined, *N* = sample size, SVL = snout-vent length, TL = tail length, SE = standard error.

Grouping	Sex	<i>N</i>	SVL (cm)		TL (cm)		Mass (g)		
			Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range	
Female	1	F	5	20.20 (0.654)	18.6-22.0	5.42 (0.185)	4.9-5.9	7.18 (0.477)	5.40-8.10
		M	8	19.89 (0.404)	17.9-21.3	5.94 (0.124)	5.4-6.3	6.50 (0.462)	4.20-8.20
		U	1	17.3	–	5.9	–	3.1	–
		Combined	14	19.81 (0.369)	17.3-22.0	5.75 (0.115)	4.9-6.3	6.50 (0.409)	3.10-8.20
	2	F	12	24.08 (0.165)	23.2-25.0	6.92 (0.063)	6.5-7.2	10.90 (0.146)	9.80-11.40
		M	5	23.98 (0.379)	22.8-24.9	7.74 (0.157)	7.2-8.1	10.92 (0.224)	10.30-11.60
		Combined	17	24.05 (0.154)	22.8-25.0	7.16 (0.11)	6.5-8.1	10.91 (0.118)	9.78-11.57
	3	F	3	22.60 (0.306)	22.2-23.2	6.10 (0.300)	5.8-6.7	9.05 (0.161)	8.70-9.30
		M	9	23.41 (0.134)	22.8-24.2	7.09 (0.096)	6.8-7.6	9.49 (0.113)	9.00-10.10
		Combined	12	23.21 (0.159)	22.2-24.2	6.84 (0.161)	5.8-7.6	9.38 (0.107)	8.74-10.09
	Sex	F	20	22.88 (0.417)	18.6-25.0	6.42 (0.163)	4.9-7.2	9.69 (0.390)	5.40-11.40
		M	22	22.26 (0.429)	17.9-24.9	6.82 (0.169)	5.4-8.1	8.73 (0.424)	4.20-11.57
All neonates	–	43	22.44 (0.318)	17.3-25.0	6.61 (0.119)	4.9-8.1	9.05 (0.322)	3.10-11.57	

TABLE 11. ANOVA summaries examining sex and litter differences in neonate snout-vent length (SVL), neonate mass, and neonate tail length (TL) for three *Nerodia rhombifer* litters from Hidalgo County, Texas. The ANOVA design was a two-level mixed model ANOVA treating sex as the fixed factor and litter as a random effect. Snout-vent-length was used as a covariate for the analyses of mass and TL. df = degrees of freedom, SS = sum of squares, MS = mean squares,  $F$  =  $F$ -ratio,  $P$  = probability that null hypothesis is true

Test	Source	df	SS	MS	$F$	$P$
SVL	Sex	1	0.155	0.155	0.005	0.944
	Litter within sex	4	125.031	31.258	43.266	< 0.001
	Error	36	26.008	0.722		
	Total	41				
Mass	SVL (covariate)	1	10.060	10.060	31.243	< 0.001
	Sex	1	0.210	0.210	0.132	0.736
	Litter within sex	4	5.583	1.396	4.335	0.006
	Error	35	11.270	0.322		
	Total	41				
TL	SVL (covariate)	1	1.588	1.588	25.467	< 0.001
	Sex	1	4.661	4.661	13.651	0.023
	Litter within sex	4	1.197	0.299	4.800	0.003
	Error	35	2.182	0.0623		
	Total	41				

TABLE 12. Regression equations and coefficients of determination for all five models fitted to growth data for *Nerodia rhombifer* from Willow Lake, Santa Ana National Wildlife Refuge. The models are listed in order of decreasing explained variation in growth rate by size. The slopes show that growth rates decrease with size. Calculation of growth rate ( $GR$ ), specific growth rate ( $G$ ), geometric mean  $SVL$  ( $S$ ), and  $\overline{SVL}$  are described in Van Devender, (1978) and Kaufmann (1981). F = female, M = male,  $N$  = sample size,  $R^2$  = coefficient of determination,  $P$  = probability that the null hypothesis is true.

Model	Sex	$N$	Equation	$R^2$	$P$
Power	F	39	$\ln G = -3.368 \ln S + 14.730$	0.507	< 0.001
	M	28	$\ln G = -3.373 \ln S + 14.409$	0.401	< 0.001
Logistic	F	39	$G = -3.97E-6 S + 0.00419$	0.375	< 0.001
	M	28	$G = -3.92E-6 S + 0.00366$	0.269	0.005
Gompertz	F	39	$G = -0.00284 \ln S + 0.01996$	0.369	< 0.001
	M	28	$G = -0.00233 \ln S + 0.01617$	0.246	0.007
Bertalanffy	F	39	$G = 1.80 S^{-1} - 0.00139$	0.334	< 0.001
	M	28	$G = 1.24 S^{-1} - 0.00090$	0.208	0.015
Bertalanffy (Van Devender, 1978)	F	39	$GR = -0.00186 \overline{SVL} + 2.142$	0.287	< 0.001
	M	28	$GR = -0.00160 \overline{SVL} + 1.696$	0.114	0.078

TABLE 13. Estimated growth as a percent of SVL per day (specific growth rate, G) and 95 % predicted limits (P.L.) for selected SVLs. The estimates are based on the regression analyses producing the differential equations for the power model. SVL = snout-vent length.

SVL (cm)	Female		Male	
	% Growth per day	95 % P.L.	% Growth per day	95 % P.L.
35.0	0.674	0.077 - 5.925	0.475	0.053 - 4.241
40.0	0.430	0.051 - 3.601	0.303	0.037 - 2.457
45.0	0.289	0.036 - 2.338	0.203	0.027 - 1.544
50.0	0.203	0.026 - 1.600	0.143	0.020 - 1.033
55.0	0.147	0.019 - 1.141	0.103	0.015 - 0.728
60.0	0.110	0.014 - 0.842	0.077	0.011 - 0.534
65.0	0.084	0.011 - 0.639	0.059	0.009 - 0.406
70.0	0.065	0.009 - 0.497	0.046	0.007 - 0.317
75.0	0.052	0.007 - 0.394	0.036	0.005 - 0.254
80.0	0.042	0.005 - 0.319	0.029	0.004 - 0.208
85.0	0.034	0.004 - 0.261	0.024	0.003 - 0.173
90.0	0.028	0.004 - 0.217	0.020	0.003 - 0.146
95.0	0.023	0.003 - 0.182	0.016	0.002 - 0.125
100.0	0.0196	0.0025 - 0.155		
105.0	0.0167	0.0021 - 0.133		
110.0	0.0142	0.0018 - 0.115		
115.0	0.0123	0.0015 - 0.100		
120.0	0.0106	0.0013 - 0.088		
125.0	0.0093	0.0011 - 0.078		

TABLE 14. Mean snout-vent length (SVL), body mass, and fatbody mass for male and female *Nerodia rhombifer* collected from Hidalgo County, Texas.

		Male	Female
SVL (cm)	Mean	64.73	89.25
	SE	0.94	1.42
	Range	51.8-78.8	75.5-112.7
	<i>N</i>	52	43
Body Mass (g)	Mean	241.646	718.883
	SE	10.996	39.350
	Range	86.14-481.43	364.10-1563.47
	<i>N</i>	52	42
Fatbody Mass (g)	Mean	14.5339	36.7422
	SE	1.4815	4.2104
	Range	0.966-54.718	1.332-130.769
	<i>N</i>	52	42



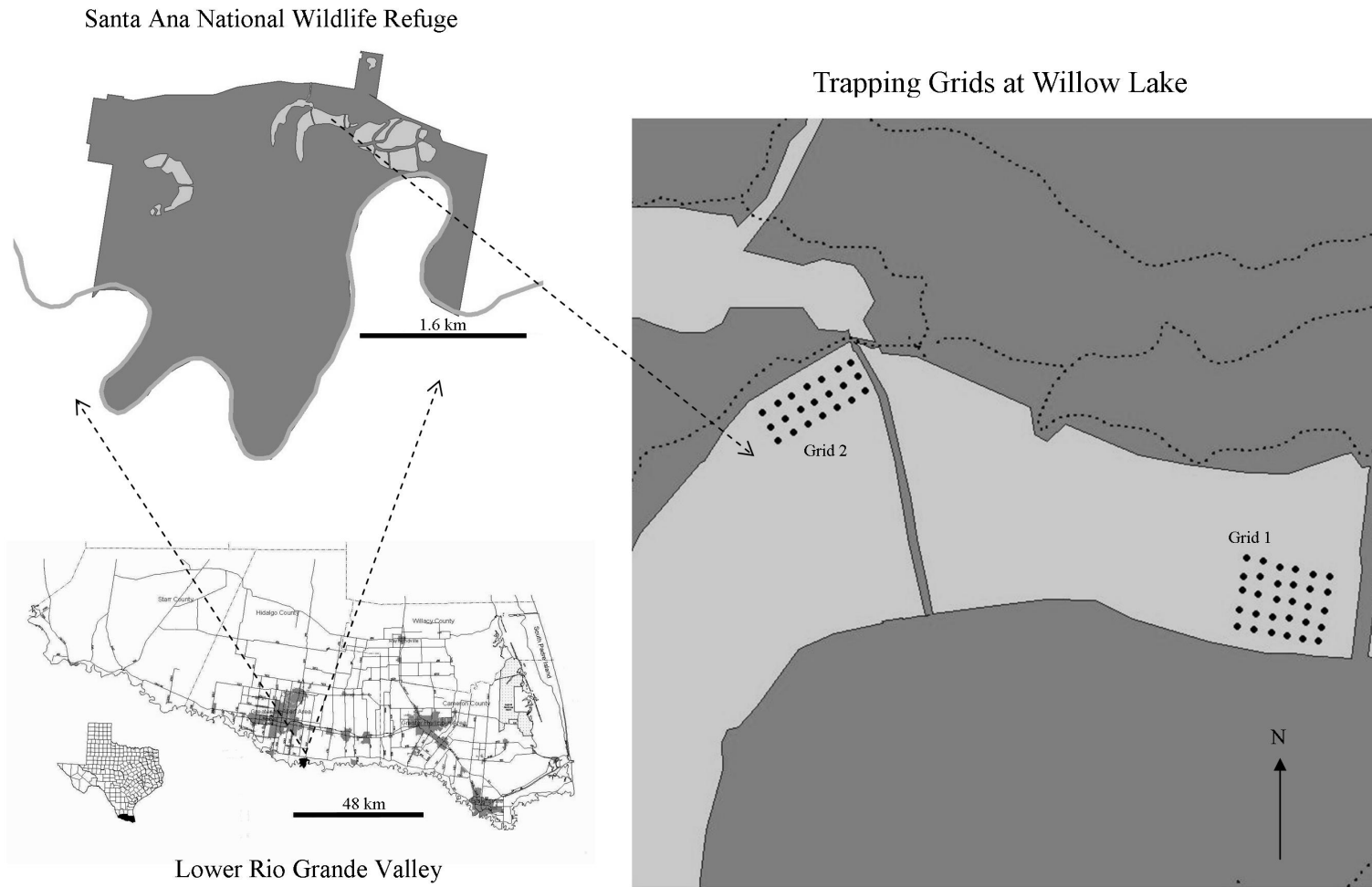


FIG. 1. Map of the study site displaying the location and arrangement of each of two trapping grids.

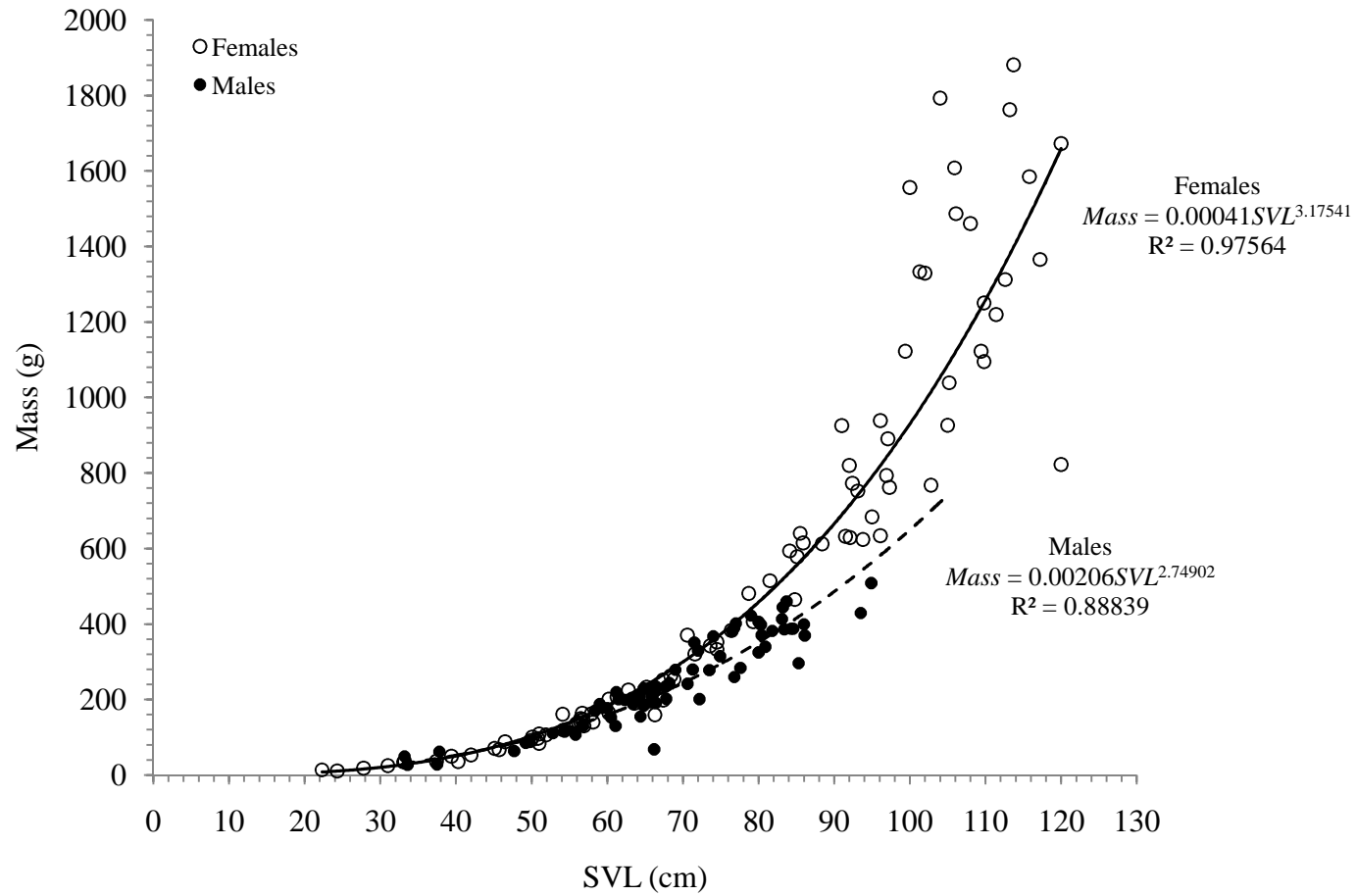


FIG. 2. Mass versus snout-vent length (SVL) for *Nerodia rhombifer* captured at Willow Lake, Santa Ana National Wildlife Refuge from August 1995 to December 1998.  $R^2$  = coefficient of determination.

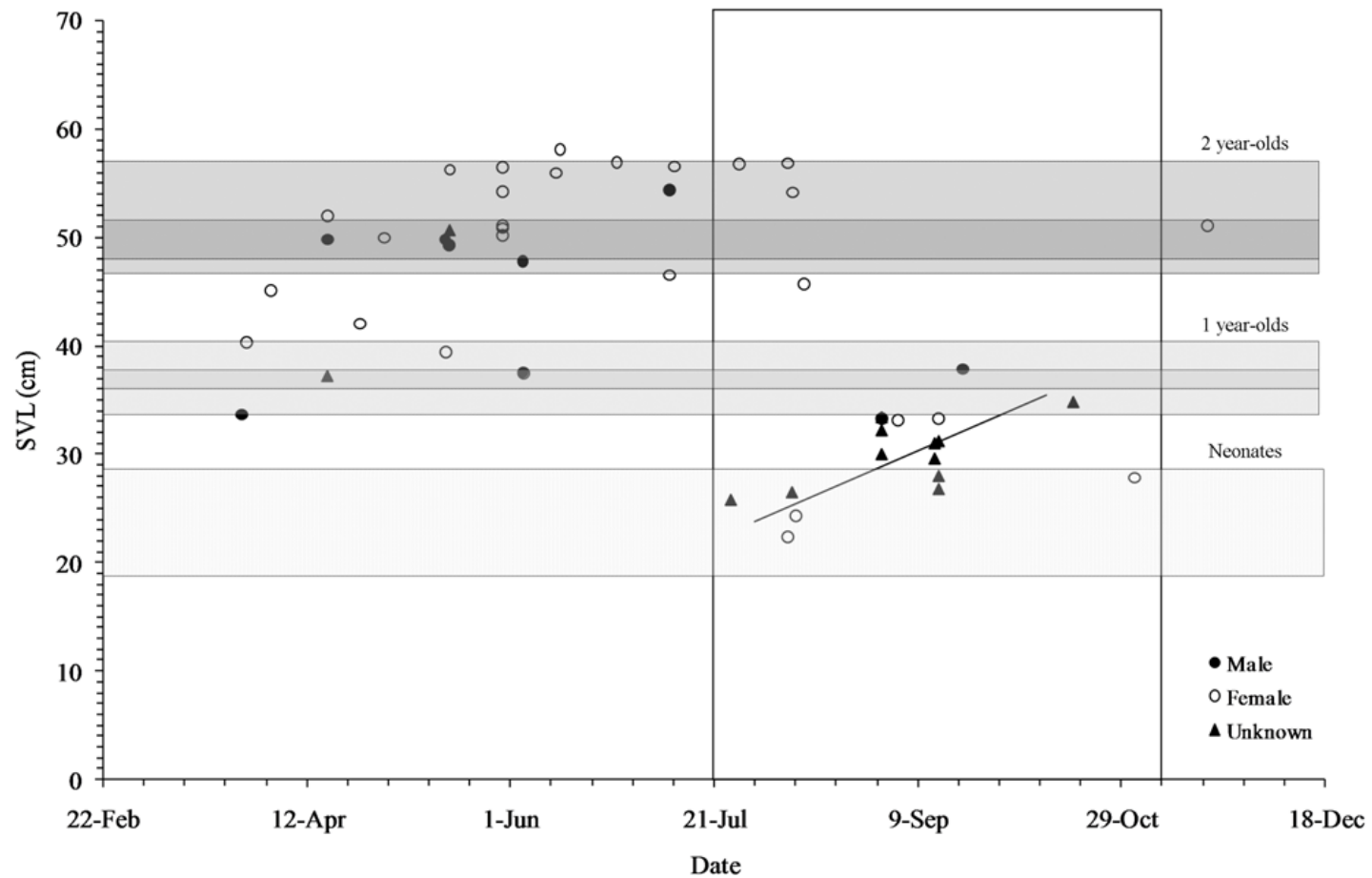


FIG. 3. Size of Willow Lake *Nerodia rhombifer* versus date of capture. The horizontal windows represent the approximate size ranges for neonates, 1 year-olds, and 2 year-olds reported by Scudder-Davis and Burghardt (1996). For 1 and 2 year-olds, the top ranges represents females and the bottom, males. The vertical window represents the approximate range of birth dates reviewed by Keck (2004). SVL = snout-vent length.

FIG. 4. (A) Monthly comparisons of the number of Willow Lake *Nerodia rhombifer* captured with expected values generated from trapping effort. Data are combined across years by month. The numbers of captures among months were significantly different from expected values ( $P \leq 0.001$ ). Note that because trapping effort varied among months, the numbers of captures are not directly comparable. (B) Monthly relative abundances for all Willow Lake *Nerodia rhombifer* represented as a percent of sample corrected for sampling effort. Data are combined across years by month. Dashed line represents the expected values if watersnakes were equally active throughout the year. [ $\% \text{ Sample} = \%RA = \frac{RA}{\sum RA} \times 100 = \frac{\sum \text{No. Captures} / \sum \text{No. Trapping Periods}}{\sum (\sum \text{No. Captures} / \sum \text{No. Trapping Periods})} \times 100$ . For reference,  $\sum RA = 38.65$ .]

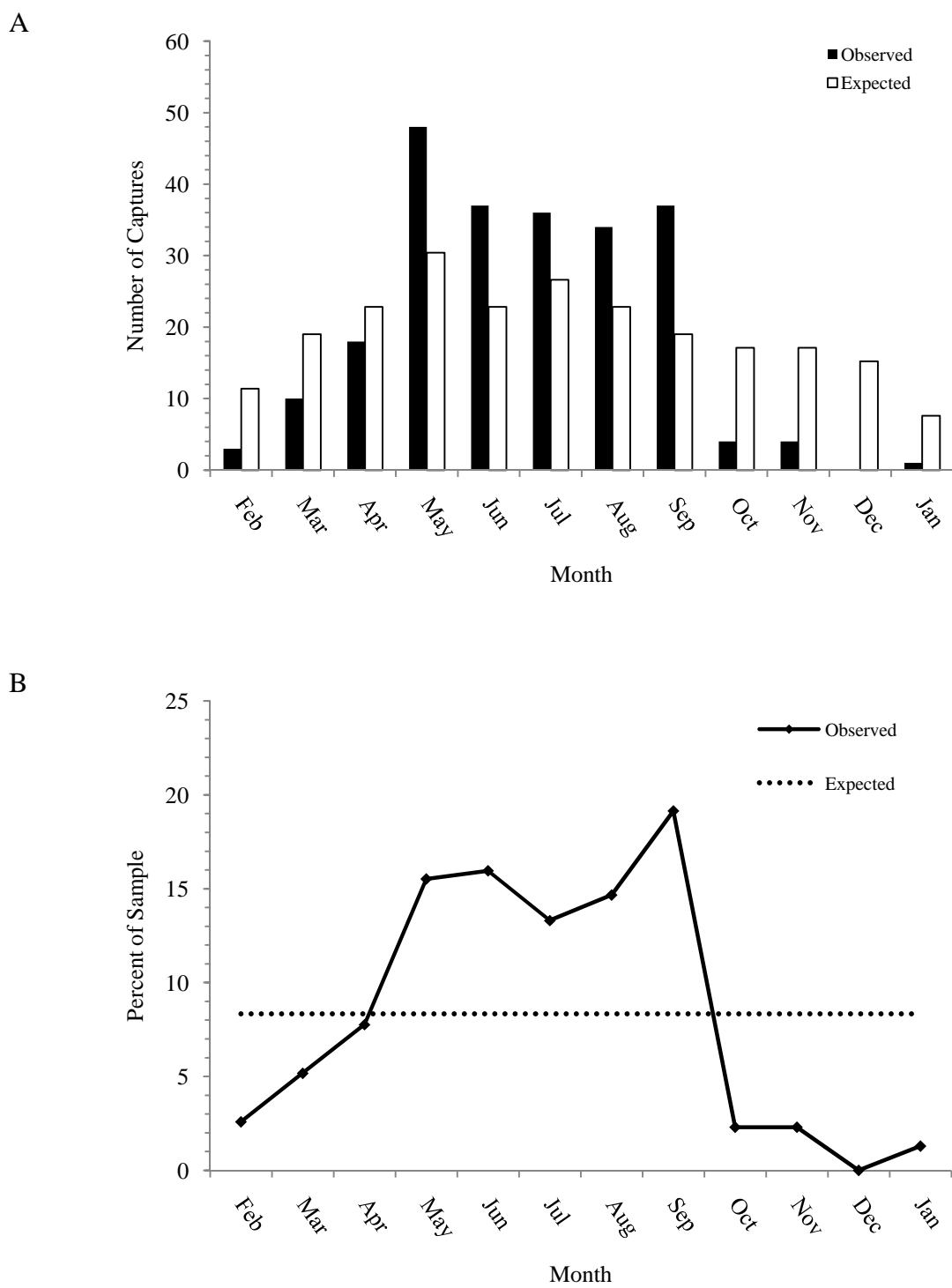


FIG. 4

FIG. 5. Monthly comparisons of the number of Willow Lake *Nerodia rhombifer* captured with expected values generated from trapping effort. Data are combined across years by month for (A) juveniles, (B) adult females, (C) and adult males. All three displayed significantly different capture rates than expected ( $P \leq 0.001$  for all three). Note that because trapping effort varied among months, the numbers of captures are not directly comparable.

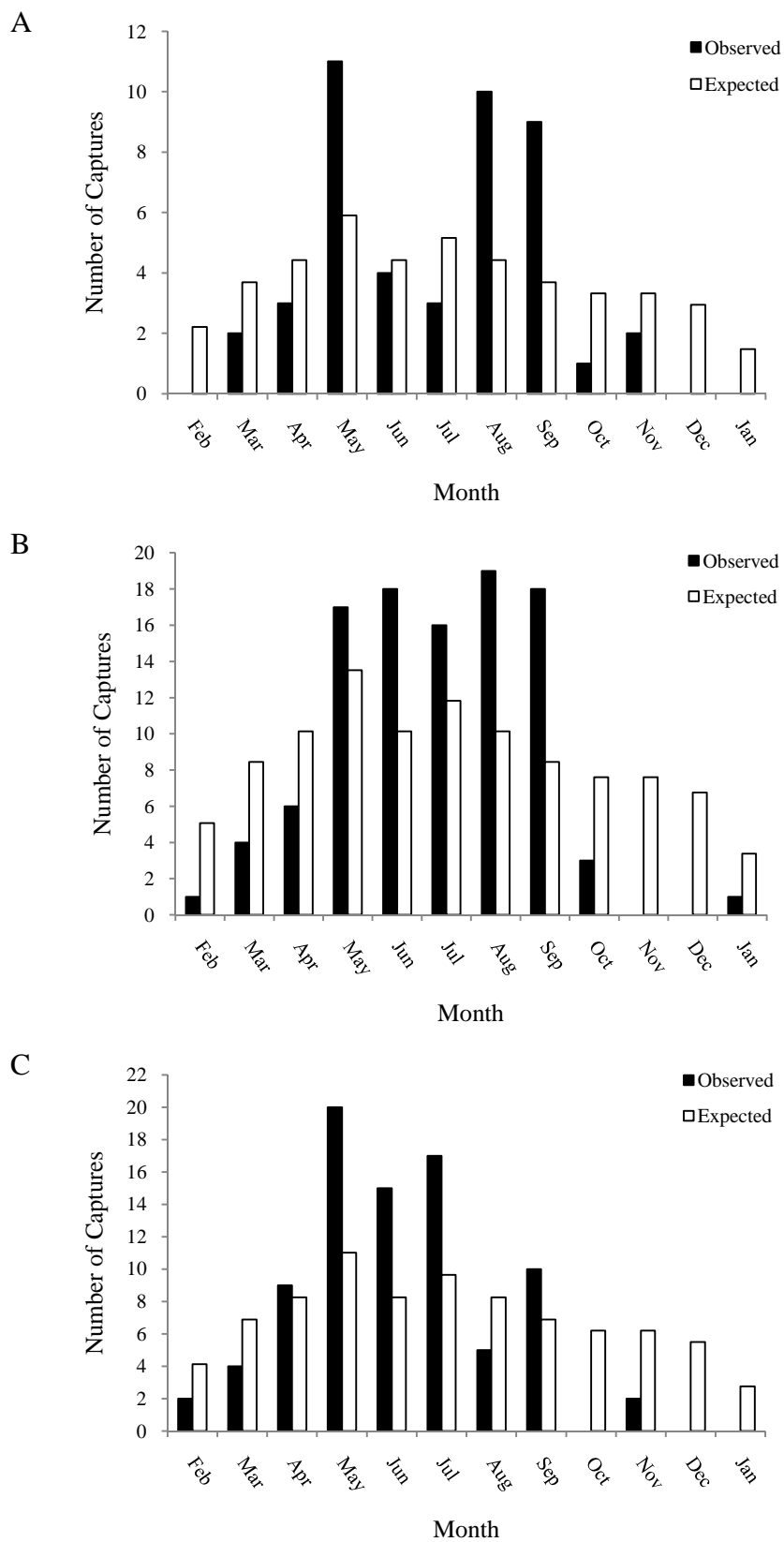


FIG. 5

Fig. 6. Monthly relative abundances of Willow Lake *Nerodia rhombifer* represented as a percent of sample corrected for sampling effort for (A) juveniles, (B) adult females, and (C) adult males. Data are combined across years by month. The dashed line in each graph represents the expected values if watersnakes were equally active throughout the year. [  $\% \text{ Sample} = \%RA = \frac{RA}{\sum RA} \times 100 = \frac{\sum \text{No. Captures} / \sum \text{No. Trapping Periods}}{\sum (\sum \text{No. Captures} / \sum \text{No. Trapping Periods})} \times 100$ . For reference,  $\sum RA = 7.50$  for juveniles,  $\sum RA = 17.48$  for adult females, and  $\sum RA = 13.67$  for adult males.]



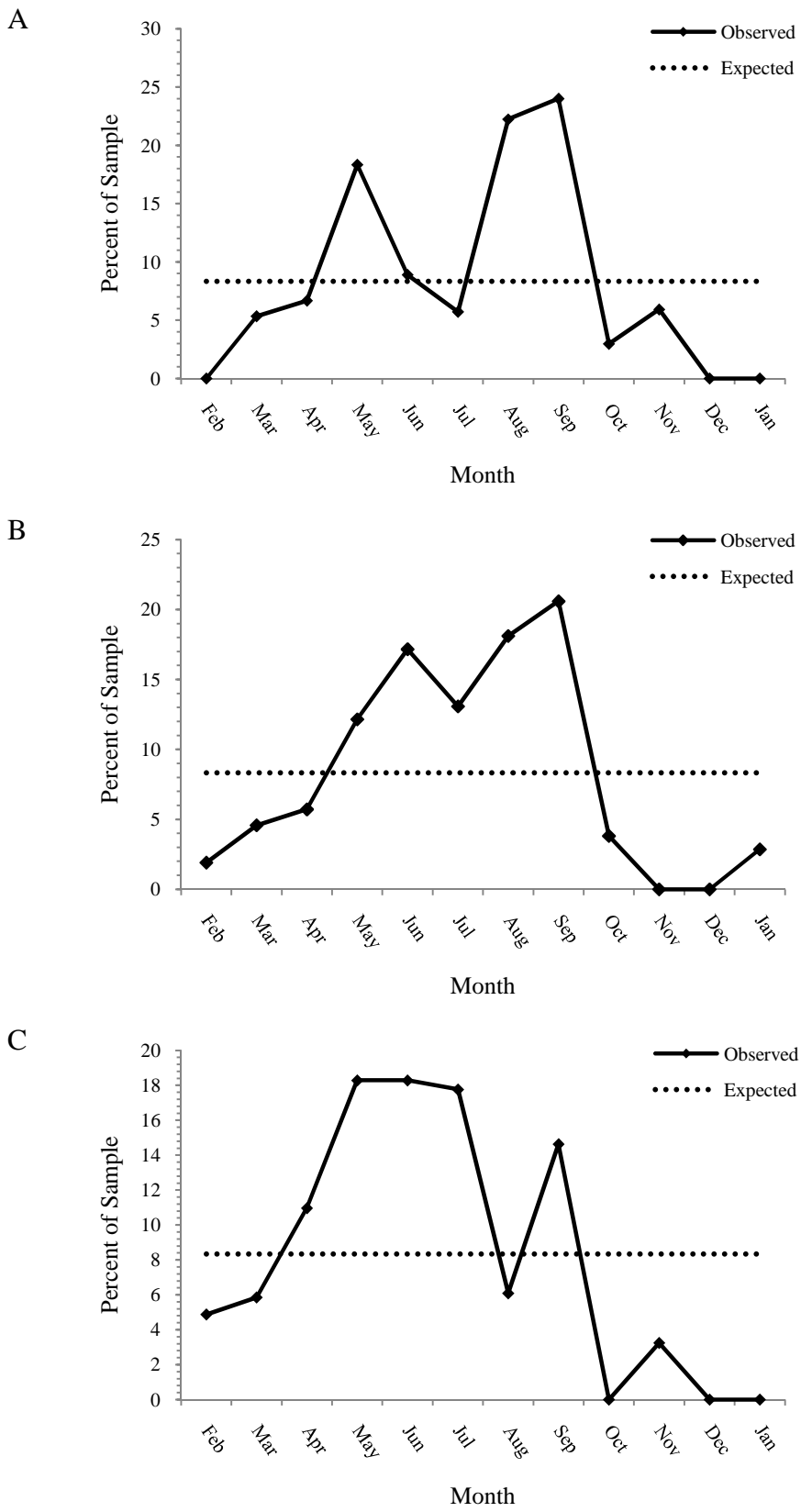


FIG. 6

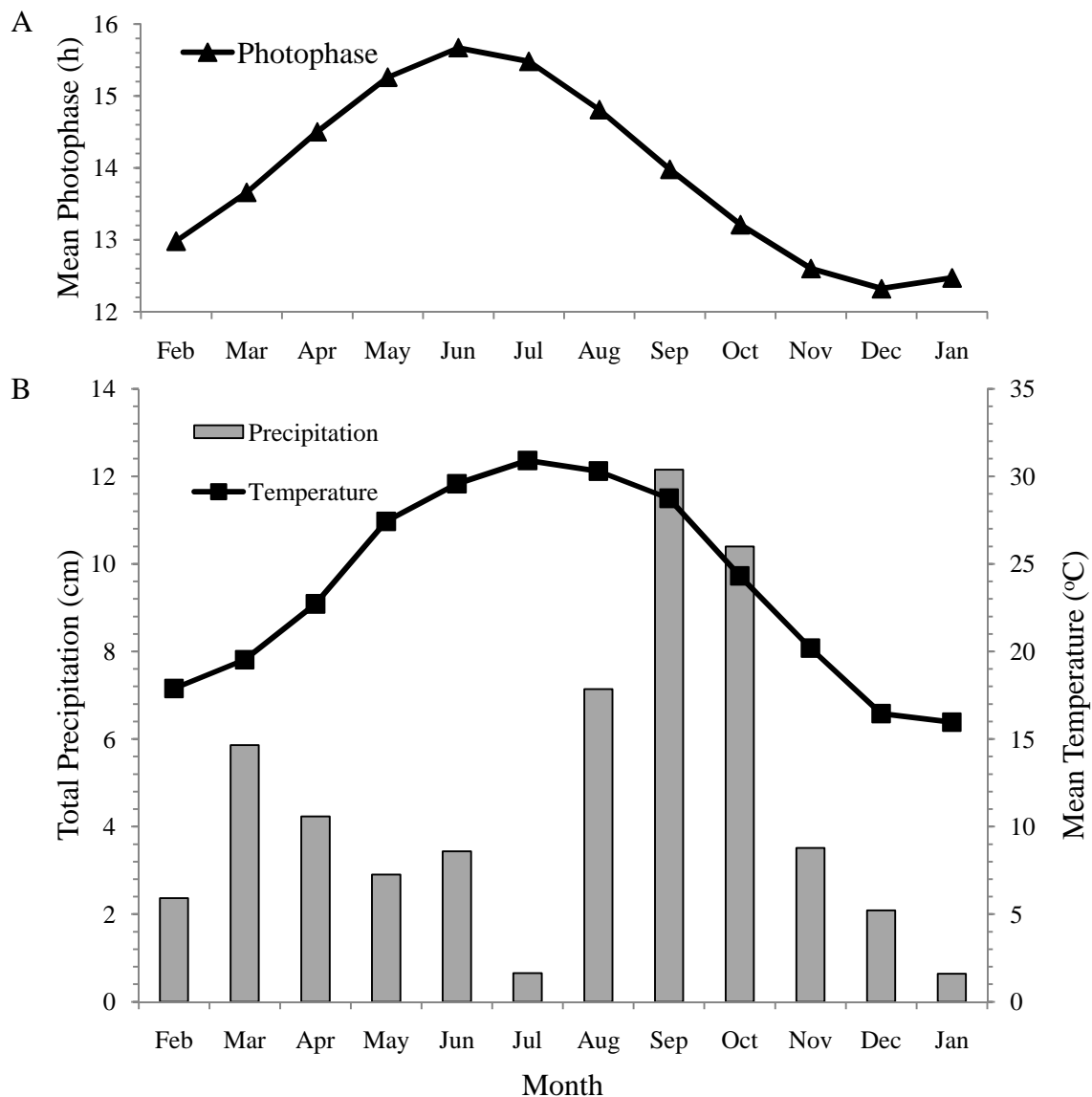


FIG. 7. (A) Mean monthly photophase, and (B) mean total monthly precipitation and mean monthly temperatures for years 1995-98. Precipitation and temperature data were from two weather stations closest to Santa Ana National Wildlife Refuge: McAllen (National Weather Service MCAT2), 17 km NNW; and Weslaco 2E (National Weather Service WEST2), 21 km ENE.

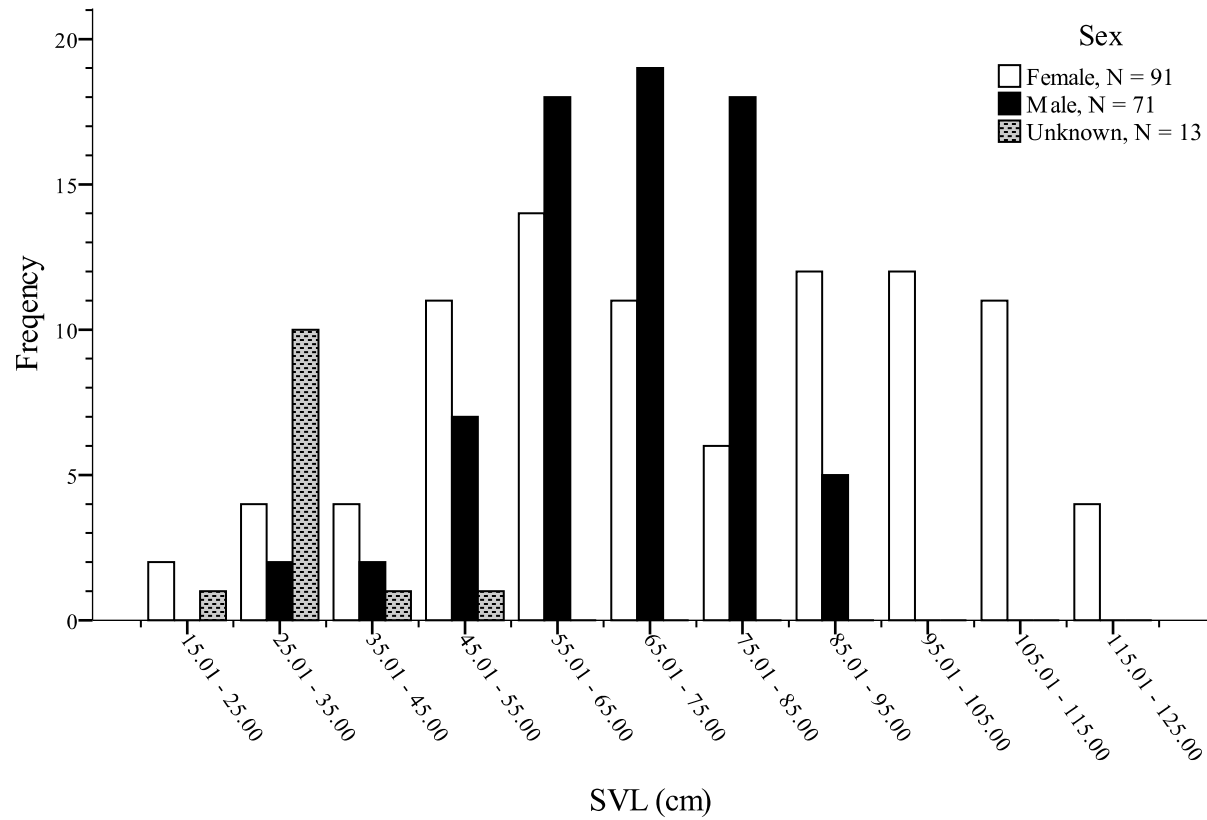


FIG. 8. Size structure for *Nerodia rhombifer* constructed from data collected from Willow Lake, Santa Ana National Wildlife Refuge from 1995-1998. N = sample size, SVL = snout-vent length.

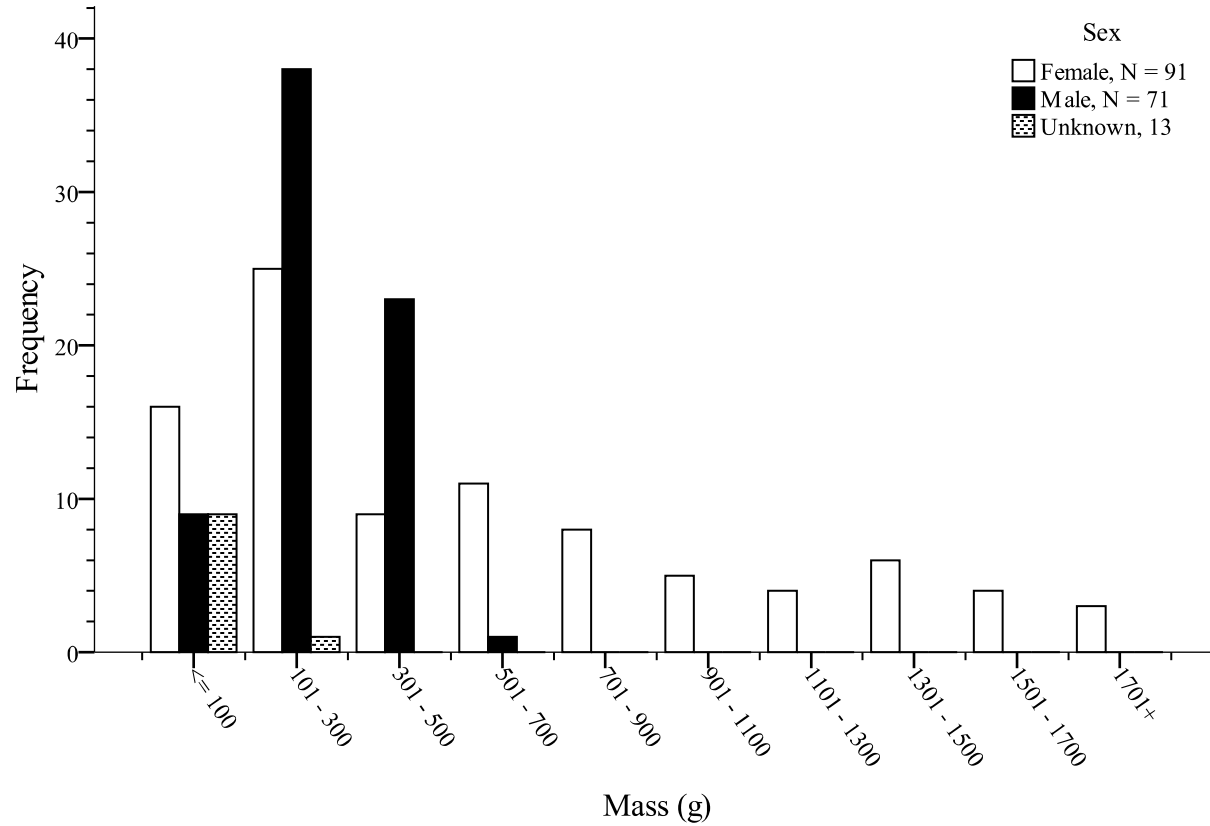


FIG. 9. Mass structure for *Nerodia rhombifer* constructed from data collected from Willow Lake, Santa Ana National Wildlife Refuge from 1995-1998. N = sample size.

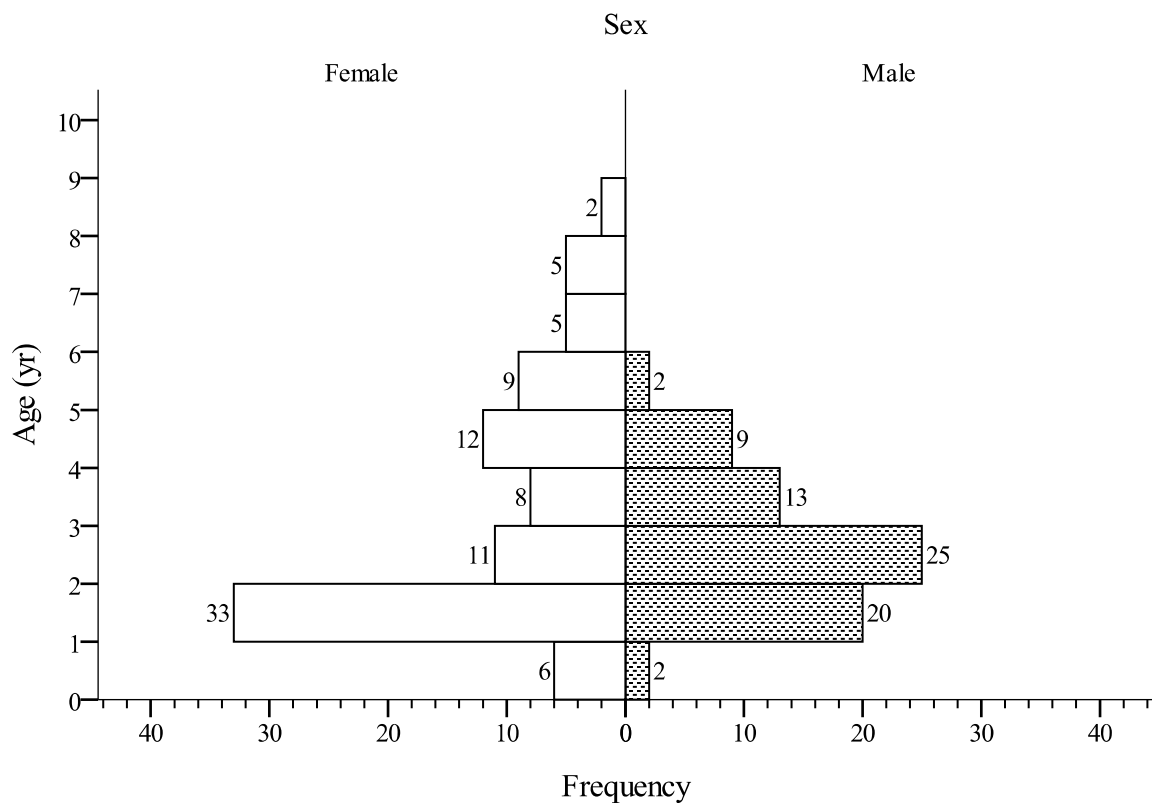


FIG. 10. Age structure for *Nerodia rhombifer* constructed from size data collected from Willow Lake, Santa Ana National Wildlife Refuge from 1995-1998. Ages for individuals used to generate the age structure were estimated from power growth models empirically fit to growth increments for females and males, separately. Numbers beside the frequency bars indicate the number of individuals assigned to each age group.

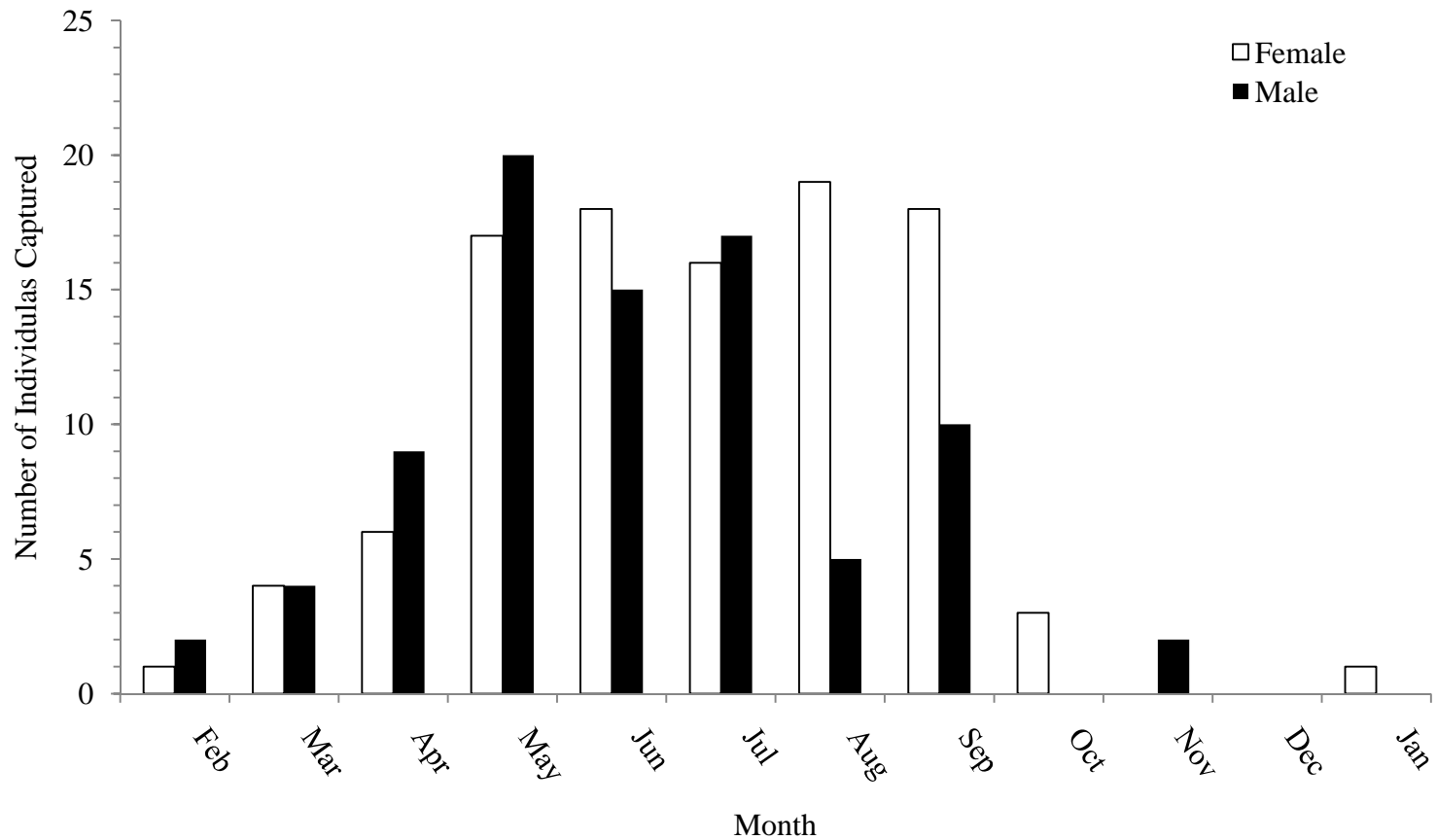


FIG. 11. Sex ratios for individual adult *Nerodia rhombifer* by month from Willow Lake, Santa Ana National Wildlife Refuge. Data are combined from years 1995-1998. Because of small sample sizes, only ratios from April to September are formally comparable. The only significantly biased sex ratio was in August, where females outnumbered males by a ratio of 1.8:1.0 ( $P = 0.008$ ).

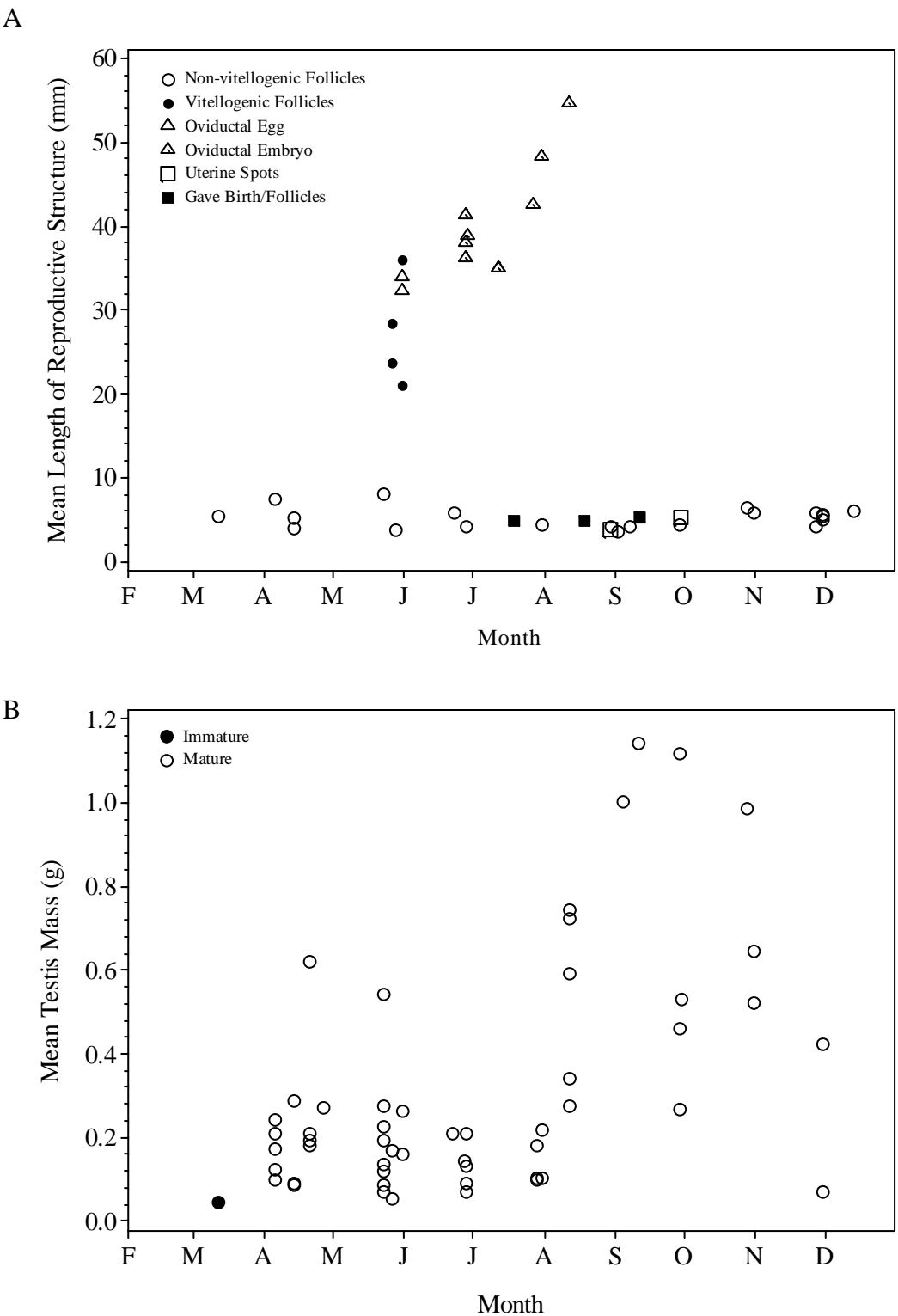


Fig. 12. (A) Size of reproductive structures for female *Nerodia rhombifer*  $\geq 75.5$  cm SVL collected in irrigation canals in Hidalgo County, Texas. (B) Mean mass of testes for male *Nerodia rhombifer*  $\geq 48.4$  cm SVL collected in irrigation canals in Hidalgo County, Texas. SVL = snout-vent length.

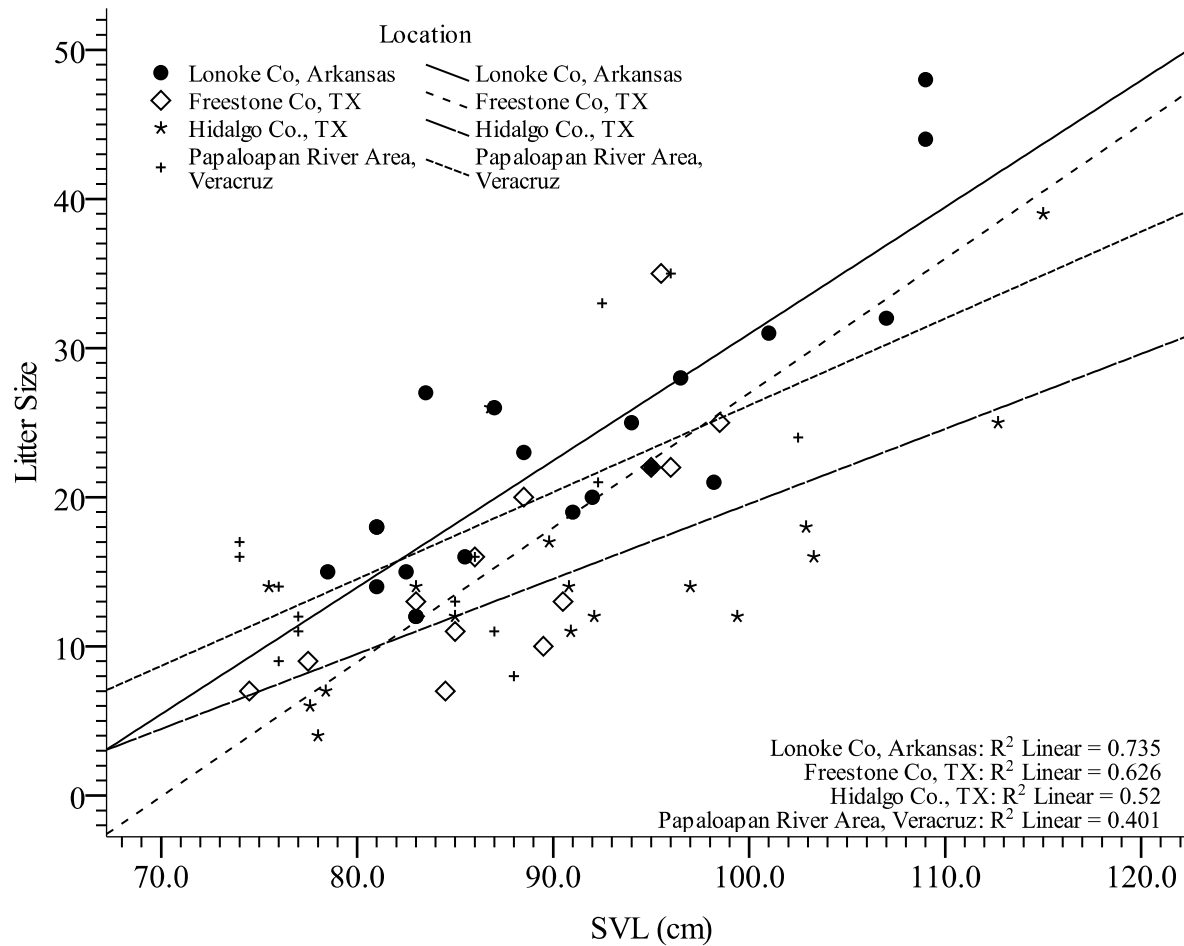


FIG. 13. Comparison of regression lines of litter sizes versus maternal snout-vent lengths (SVL) for *Nerodia rhombifer* from Hidalgo County, Texas and three other populations from temperate and tropical regions. Data for the other three populations are from Plummer (1992), Aldridge et al. (1995), and M. Keck (unpublished data). The slopes were not significantly different ( $F_{3,57} = 1.69$ ,  $P = 0.179$ ).



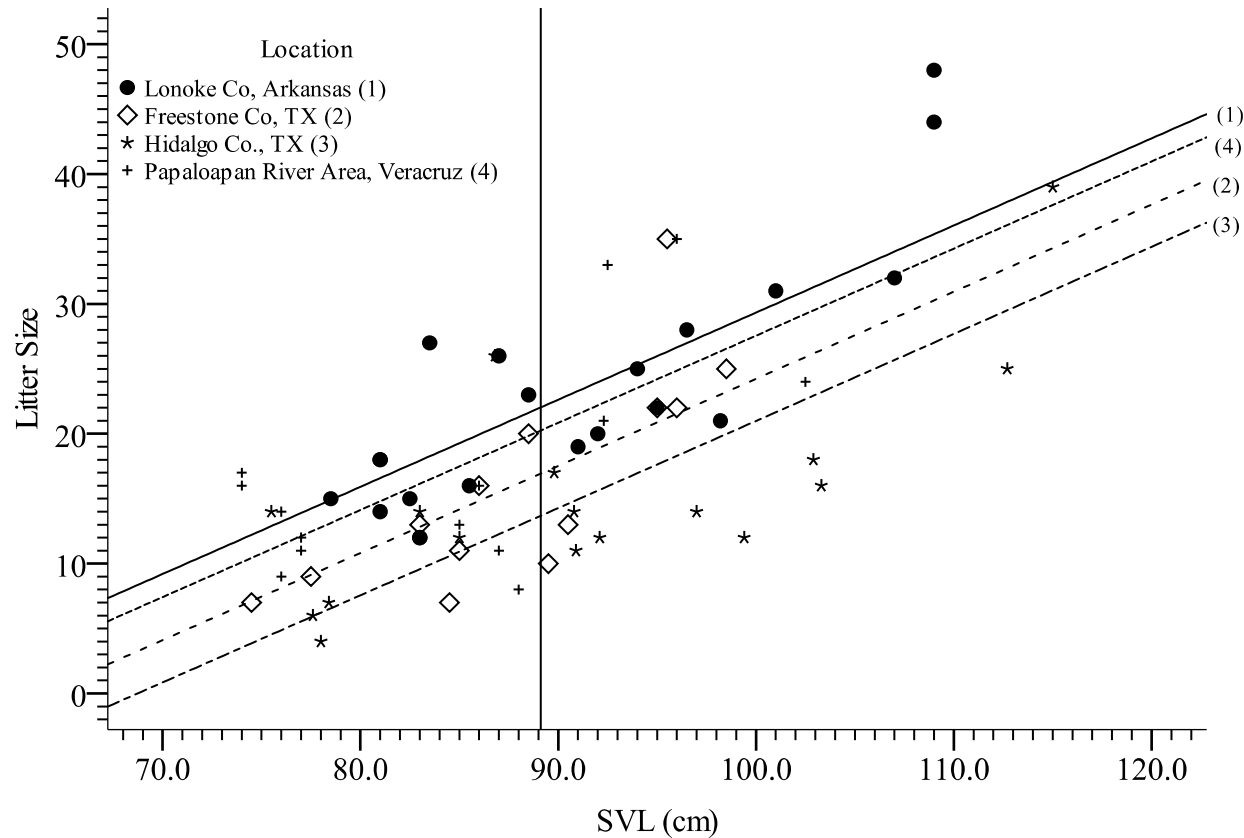


FIG. 14. Comparison of common slope models and marginal mean SVLs for Hidalgo County, Texas *Nerodia rhombifer* and three other populations from temperate and tropical regions. Models by location are identified by number in parentheses. Data for the other populations are from Plummer (1992), Aldridge et al. (1995), and M. Keck (unpublished data). Marginal means ( $\pm 1SE$ ) are compared at 89.12 cm SVL (vertical line). Significant comparisons are by location number. Lonoke Co., AK ( $N = 21$ ,  $22.0 \pm 1.28$ , Location 1): 3\*\*\*; Freestone Co., TX ( $N = 13$ ;  $16.9 \pm 1.62$ , Location 2): not significant; Hidalgo Co., TX ( $N = 17$ ,  $13.6 \pm 1.43$ , Location 3): 1\*\*\*, 4\*; Veracruz, Mex ( $N = 14$ ,  $20.2 \pm 1.60$ , Location 4): 3\*. Degree of significance is indicated by asterisks ( $P < 0.05$  indicated with \*,  $P \leq 0.001$  indicated with \*\*\*). SVL = snout-vent length.

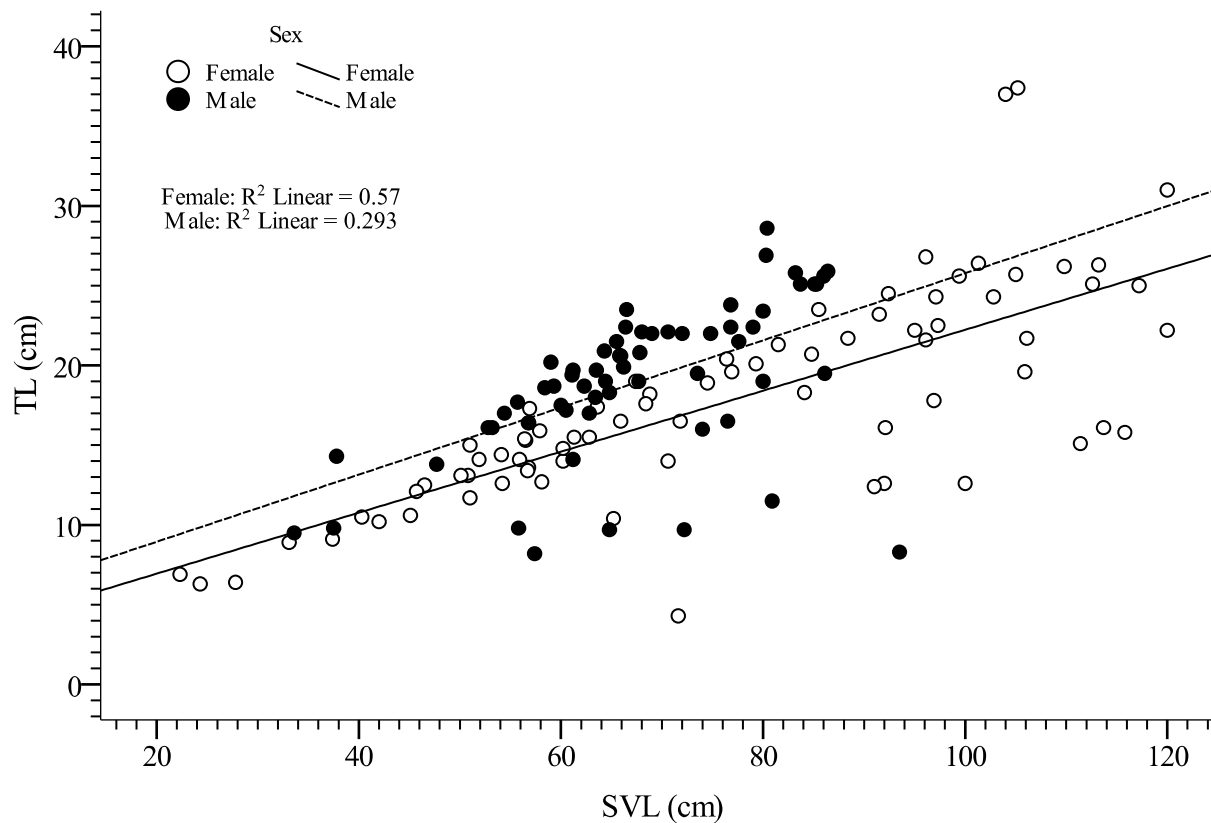


FIG. 15. Comparison of the regression lines of tail length (TL) versus snout-vent length (SVL) between male and female *Nerodia rhombifer* from Willow Lake, Santa Ana National Wildlife Refuge. An ANCOVA comparing TL using SVL as the covariate indicated that males had significantly longer tails than females proportionately ( $F_{1, 135} = 16.07, P < 0.001$ ). From the analysis, the marginal means ( $\pm$ SE) were  $19.8 \pm 0.539$  cm ( $N = 62$ ) and  $16.9 \pm 0.486$  cm ( $N = 76$ ) for males and females, respectively, and were estimated at 72.1 cm SVL.

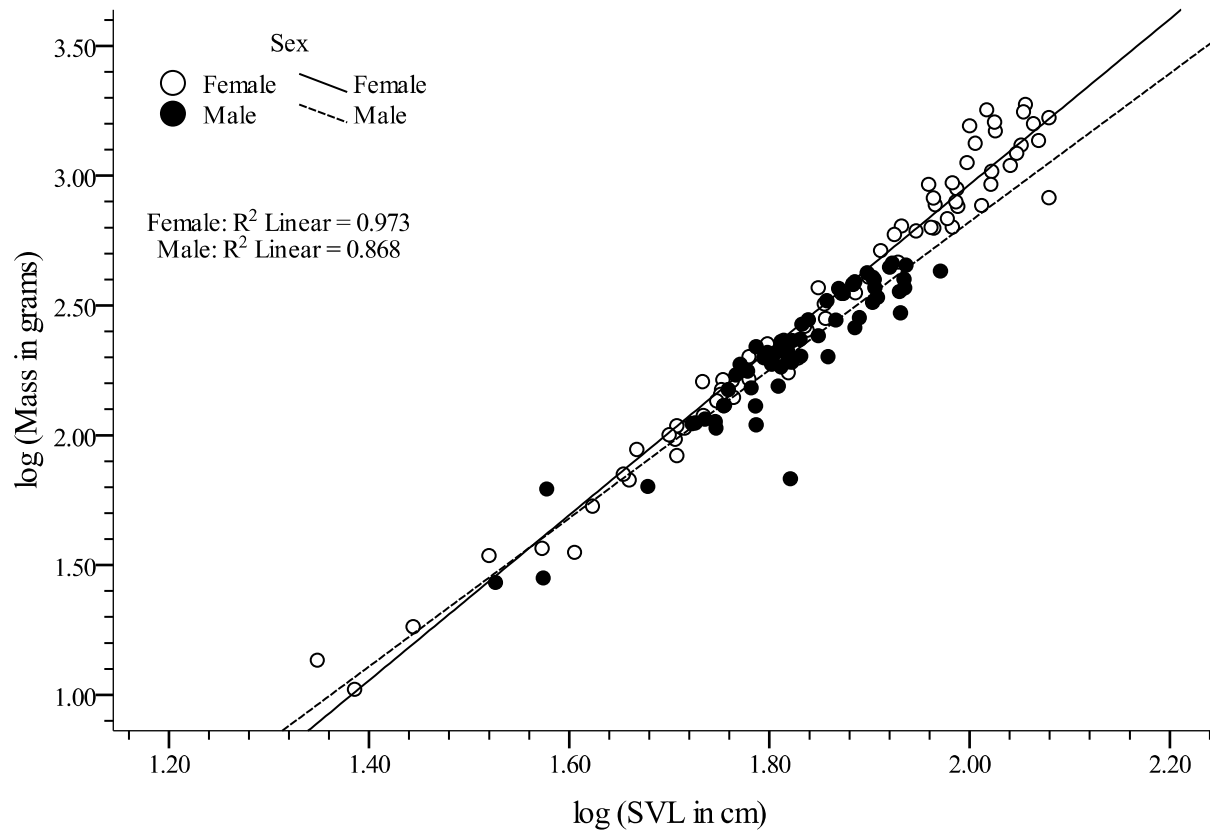


FIG. 16. Comparison of the regression lines of log(Mass in grams) versus log(SVL in cm) between male and female *Nerodia rhombifer* from Willow Lake, Santa Ana National Wildlife Refuge. A test for homogeneity of slopes was significant (GLM interaction term sex\*SVL:  $F_{1,134} = 4.75$ ,  $P = 0.031$ ) indicating that the rate of change in logMass with logSVL was not the same between the sexes. SVL = snout-vent length,  $R^2$  = coefficient of determination, GLM = general linear model.

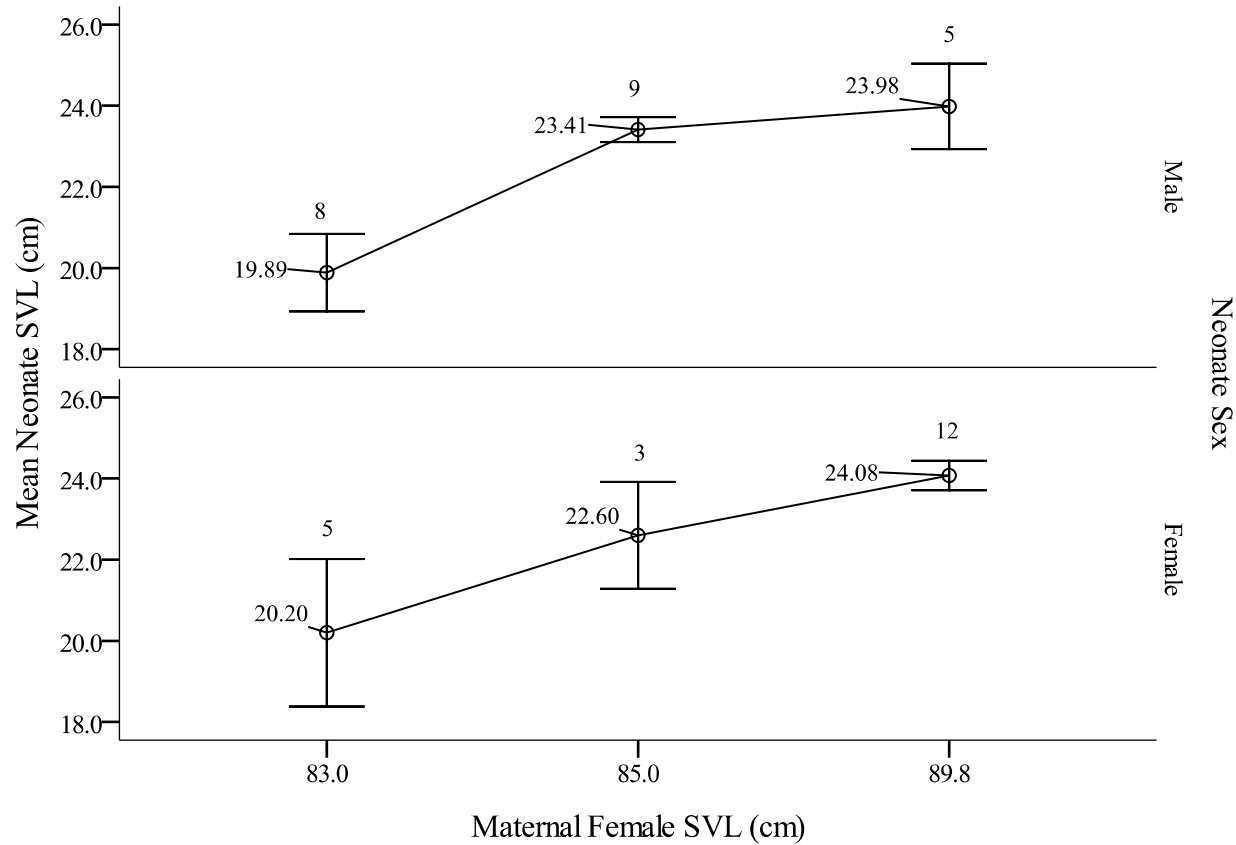


FIG. 17. A graphical comparison of mean neonate size by maternal female size for both male and female neonates for three *Nerodia rhombifer* litters from Hidalgo County, Texas. Circles are means. Error bars represent  $\pm 1SE$ . Numbers above the error bars give sample size. SVL = snout-vent length. Note that the horizontal axis is not to scale.

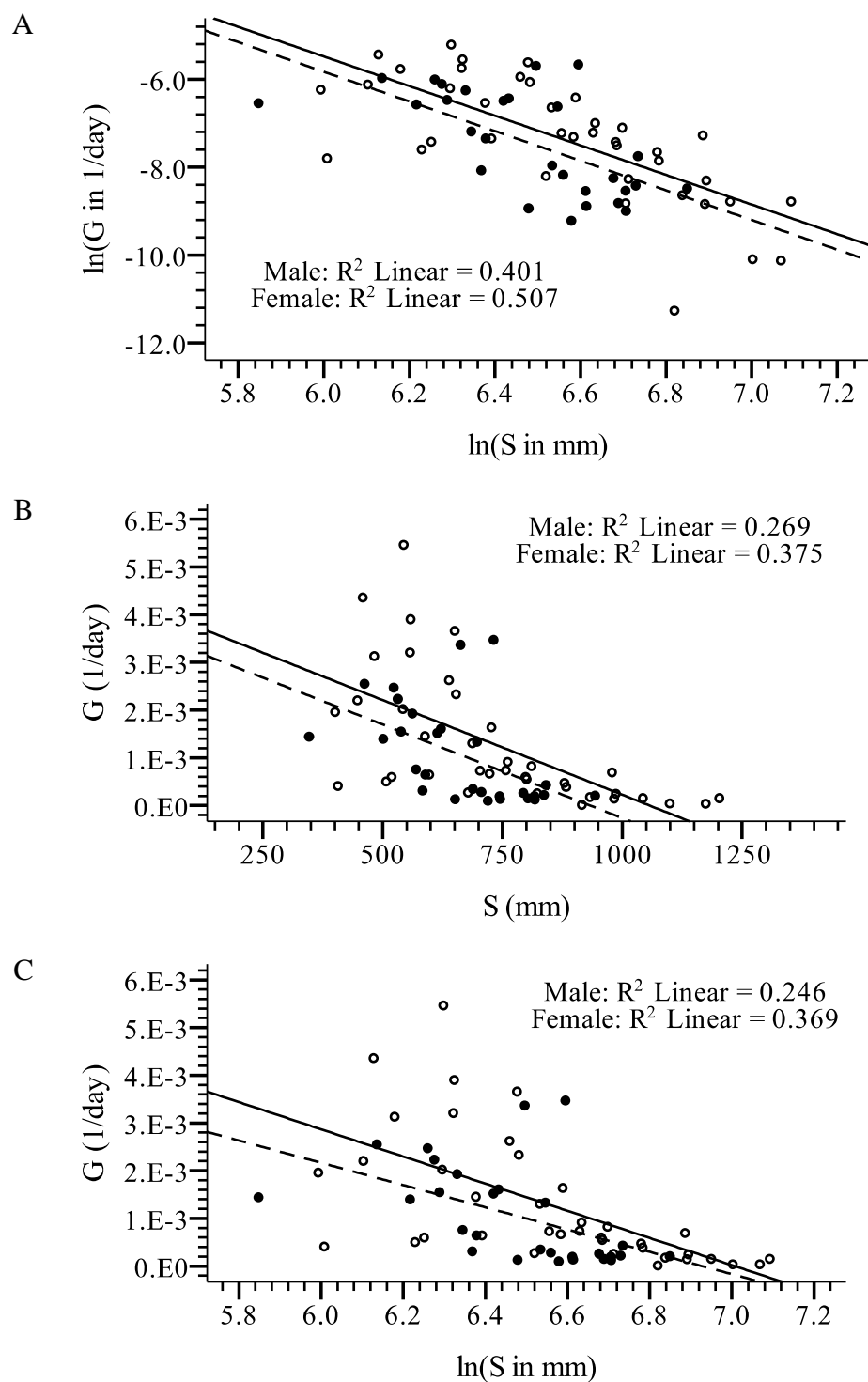


FIG. 18. Regression lines by sex (males = ●—, females = ○—) for the differential forms of the (A) power, (B) logistic, and (C) Gompertz growth models fit to growth data for *Nerodia rhombifer* from Santa Ana National Wildlife Refuge. G = specific growth rate, S = geometric mean snout-vent length for growth increment.

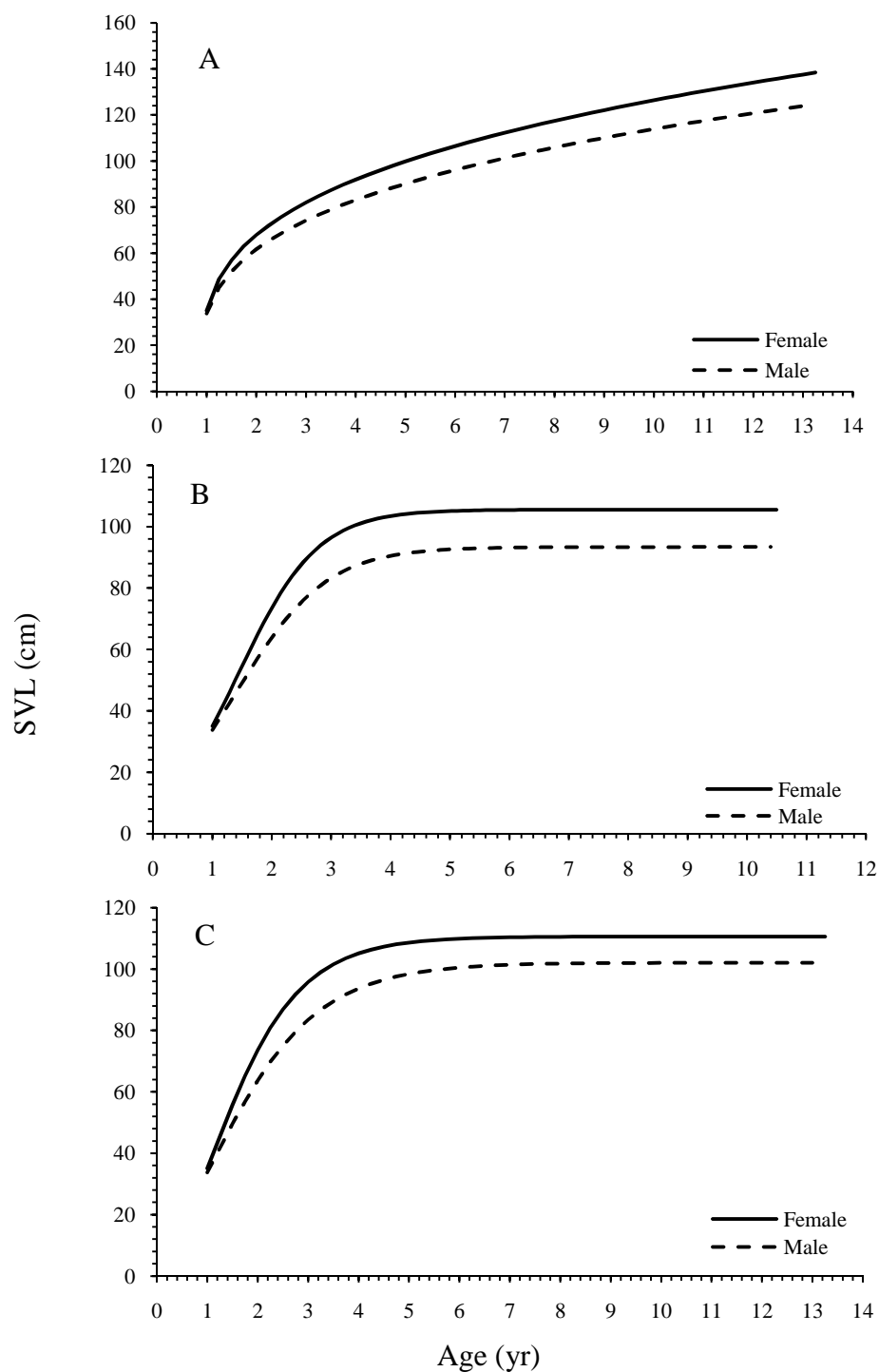


FIG. 19. Growth curves generated by integrating the regression equations estimated from field growth rates of female and male *Nerodia rhombifer* from Willow Lake, Santa Ana National Wildlife Refuge. (A) Power model; (B) Logistic model; (C) Gompertz model. Regression analyses showed that the power models explained the greatest amount of variation in size-related growth rates. SVL = snout-vent length.

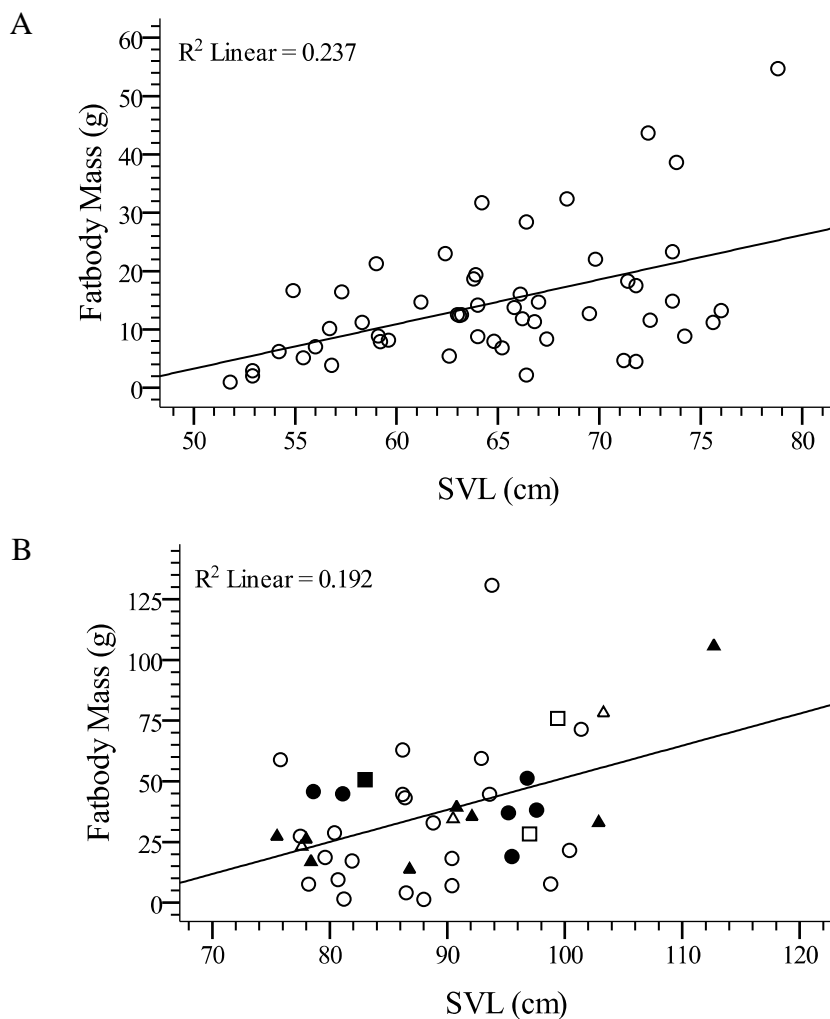


FIG. 20. The relationship between fatbody mass (FBM) and snout-vent length (SVL) for (A) adult male ( $N = 52$ ) and (B) adult female ( $N = 42$ ) *Nerodia rhombifer* collected in Hidalgo County, Texas. Only males  $\geq 51.8$  cm SVL and females  $\geq 75.5$  cm SVL were used in the analyses. The reproductive condition for individual females is indicated by symbols:  $\circ$  = quiescent,  $\bullet$  = vitellogenic,  $\triangle$  = oviductal eggs,  $\blacktriangle$  = oviductal embryos,  $\square$  = uterine spots, and  $\blacksquare$  = gave birth. For males,  $FBM = 0.764SVL - 34.9$ ,  $R^2 = 0.237$ ,  $P < 0.001$ . For females,  $FBM = 1.32SVL - 80.8$ ,  $R^2 = 0.192$ ,  $P = 0.004$ .  $R^2$  = coefficient of determination,  $P$  = probability that the null hypothesis is true.

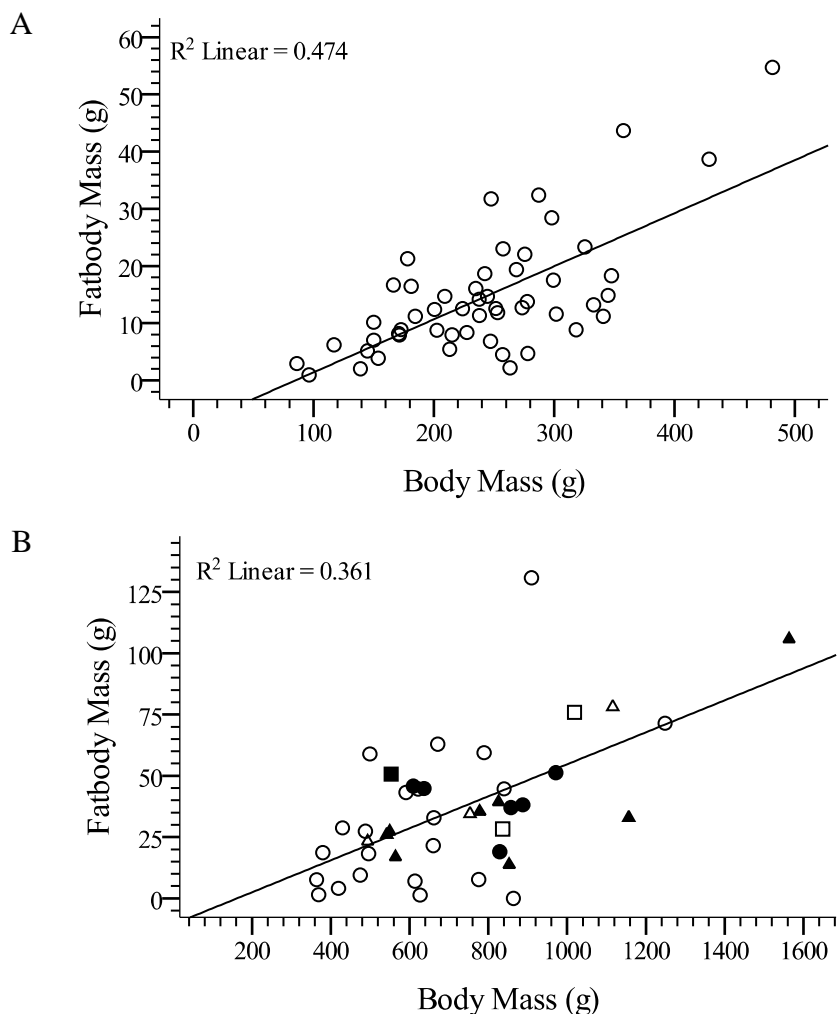


Fig. 21. The relationship between fatbody mass (FBM) and body mass (BM) for (A) adult male ( $N = 52$ ) and (B) adult female ( $N = 41$ ) *Nerodia rhombifer* collected in Hidalgo County, Texas. Only males  $\geq 51.8$  cm SVL and females  $\geq 75.5$  cm SVL were used in the analyses. The reproductive condition for individual females is indicated by symbols:  $\circ$  = quiescent,  $\bullet$  = vitellogenic,  $\triangle$  = oviductal eggs,  $\blacktriangle$  = oviductal embryos,  $\square$  = uterine spots, and  $\blacksquare$  = gave birth. For males,  $\text{FBM} = 0.096\text{BM} - 7.887$ ,  $R^2 = 0.474$ ,  $P < 0.001$ . For females,  $\text{FBM} = 0.065\text{BM} - 10.59$ ,  $R^2 = 0.361$ ,  $P < 0.001$ .  $R^2$  = coefficient of determination,  $P$  = probability that the null hypothesis is true.



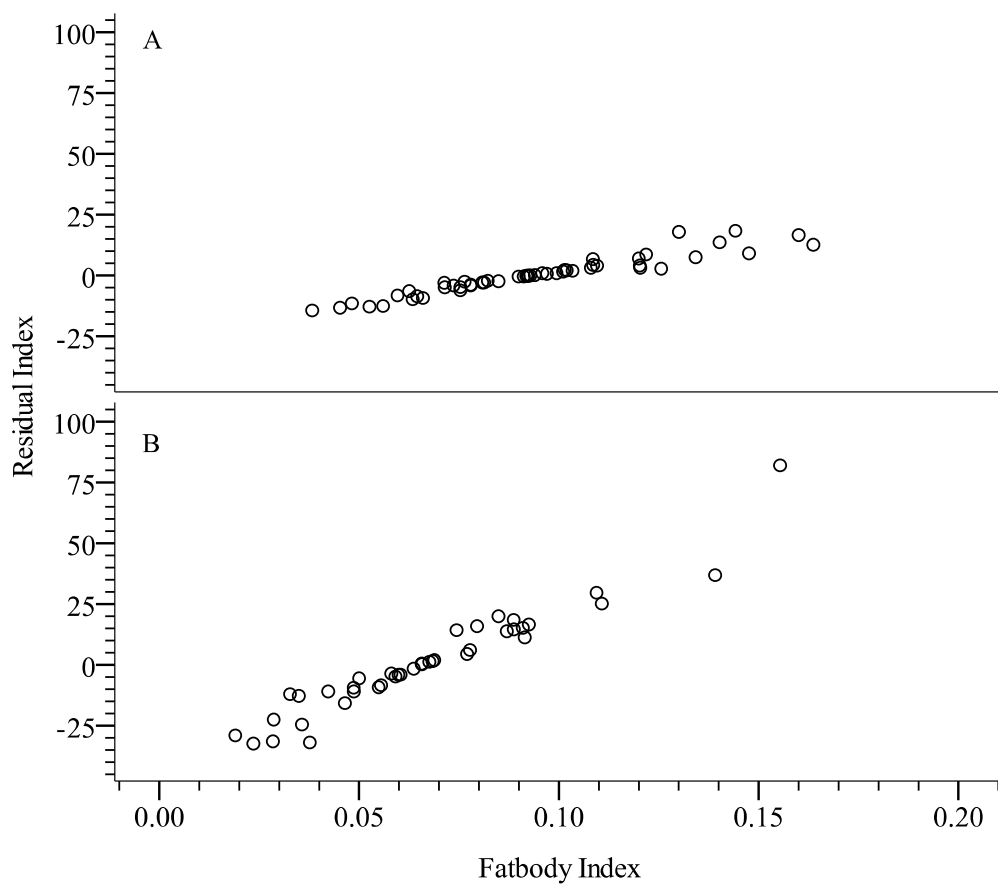


FIG. 22. Residual index versus fatbody index for (A) adult male ( $r = 0.955$ ,  $N = 52$ ,  $P < 0.001$ ) and (B) adult female ( $r = 0.964$ ,  $N = 42$ ,  $P < 0.001$ ) *Nerodia rhombifer* collected in Hidalgo County, Texas.  $r$  = correlation coefficient,  $N$  = sample size,  $P$  = probability that the null hypothesis is true.

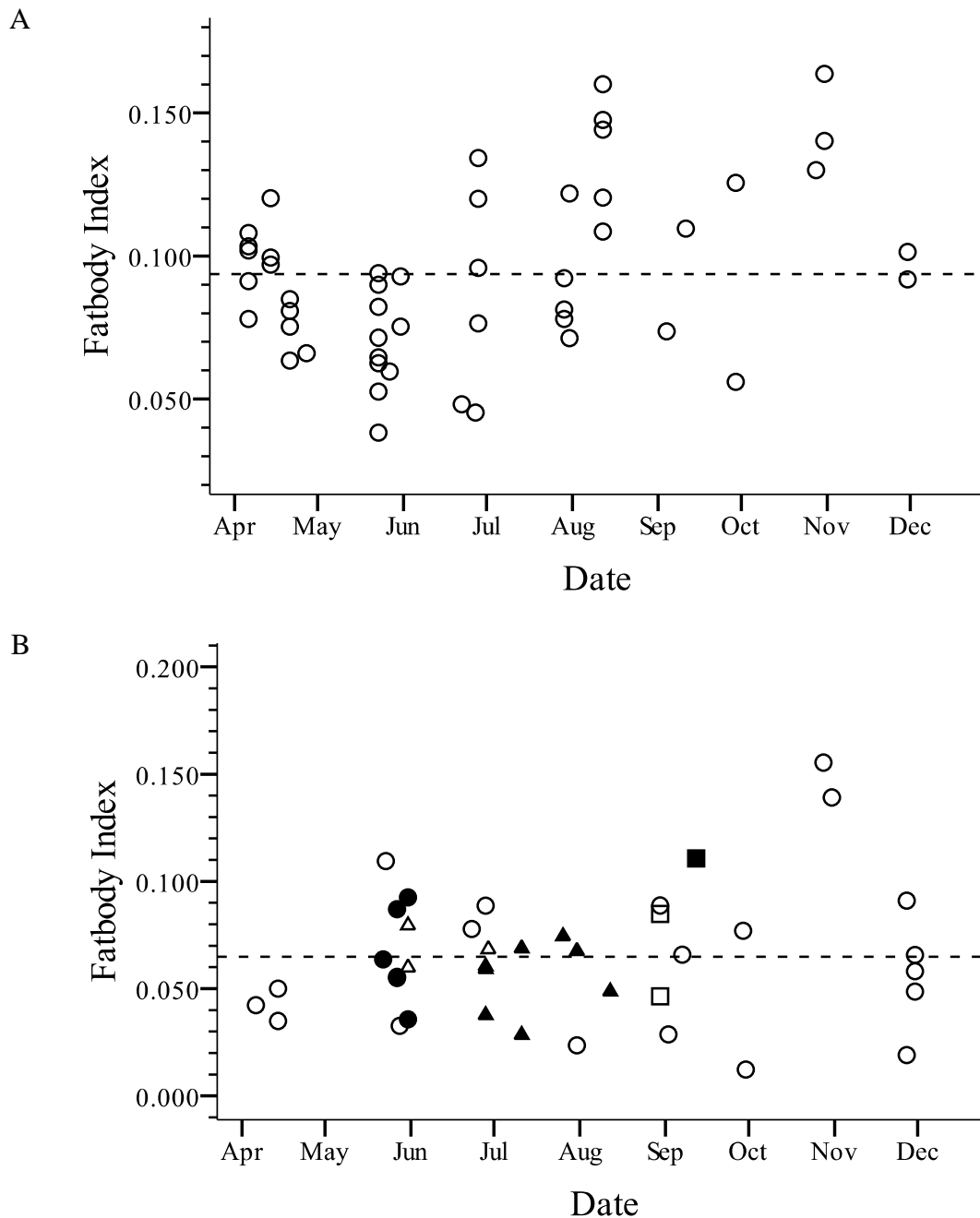


Fig. 23. Fatbody index (FBI) calculated for (A) adult male ( $N = 52$ ) and (B) adult female ( $N = 42$ ) *Nerodia rhombifer* collected in Hidalgo County, Texas. The dashed lines indicates the overall mean FBI for each sex. Only males  $\geq 51.8$  cm SVL and females  $\geq 75.5$  cm SVL were used in the analyses. The reproductive condition for individual females is indicated by symbols: ○ = quiescent, ● = vitellogenic, △ = oviductal eggs, ▲ = oviductal embryos, □ = uterine spots, and ■ = gave birth. SVL = snout-vent length.

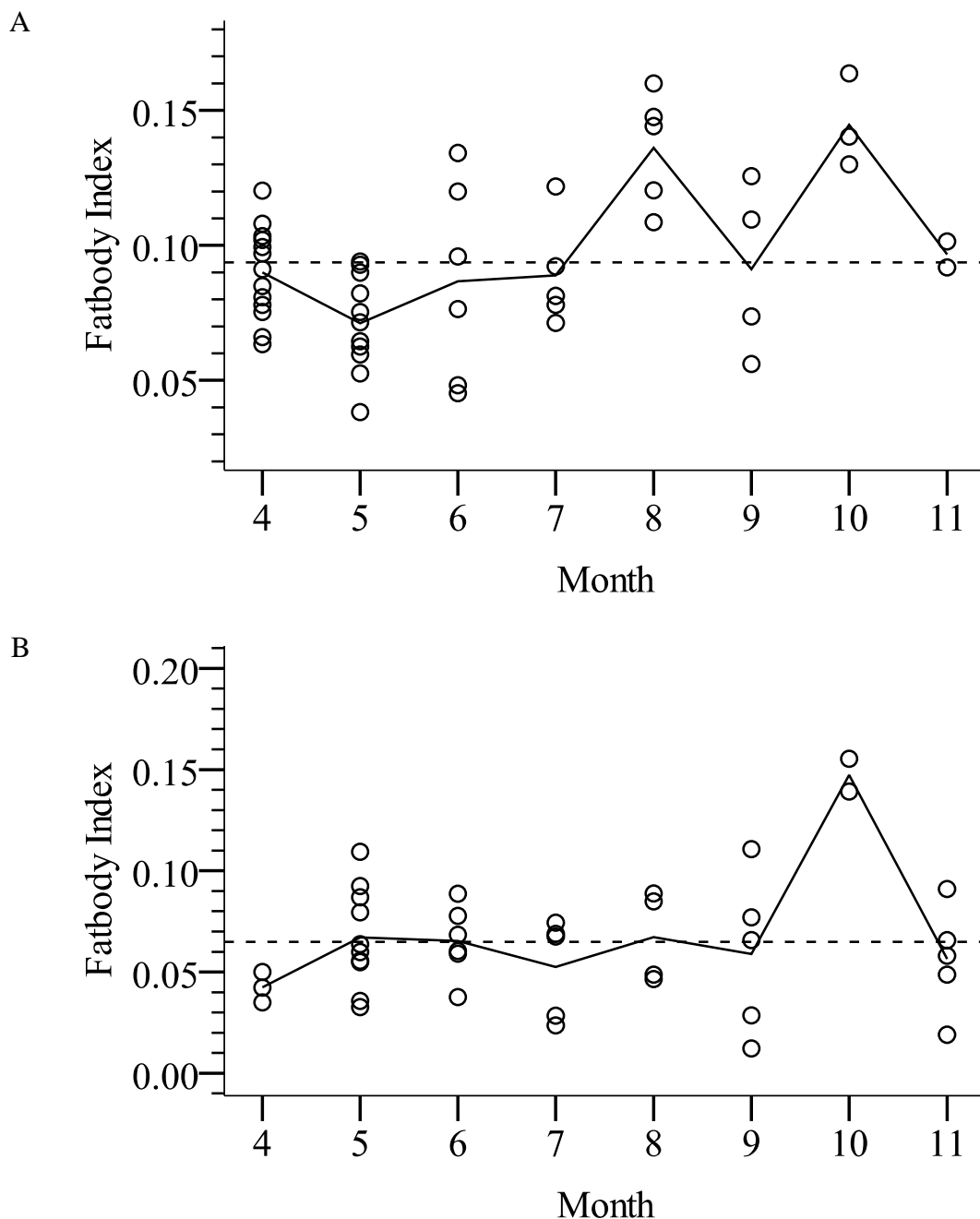


FIG. 24. Fatbody index (FBI) by month for (A) adult male ( $N = 52$ ) and (B) adult female ( $N = 42$ ) *Nerodia rhombifer* collected in Hidalgo County, Texas. The dashed lines indicate the overall mean FBI for each sex. Only males  $\geq 51.8$  cm SVL and females  $\geq 75.5$  cm SVL were used in the analyses. The interpolation lines indicate monthly means. Kruskal-Wallis Tests indicated that males displayed a significant among month difference in FBI ( $\chi^2 = 21.70$ ,  $df = 7$ ,  $P = 0.003$ ), but females did not ( $\chi^2 = 8.78$ ,  $df = 7$ ,  $P = 0.269$ ). Months are indicated by number (i.e., 4 = April, 5 = May...11 = November).  $N$  = sample size. SVL = snout-vent length,  $\chi^2$  = chi-square value,  $df$  = degrees of freedom,  $P$  = probability that the null hypothesis is correct.

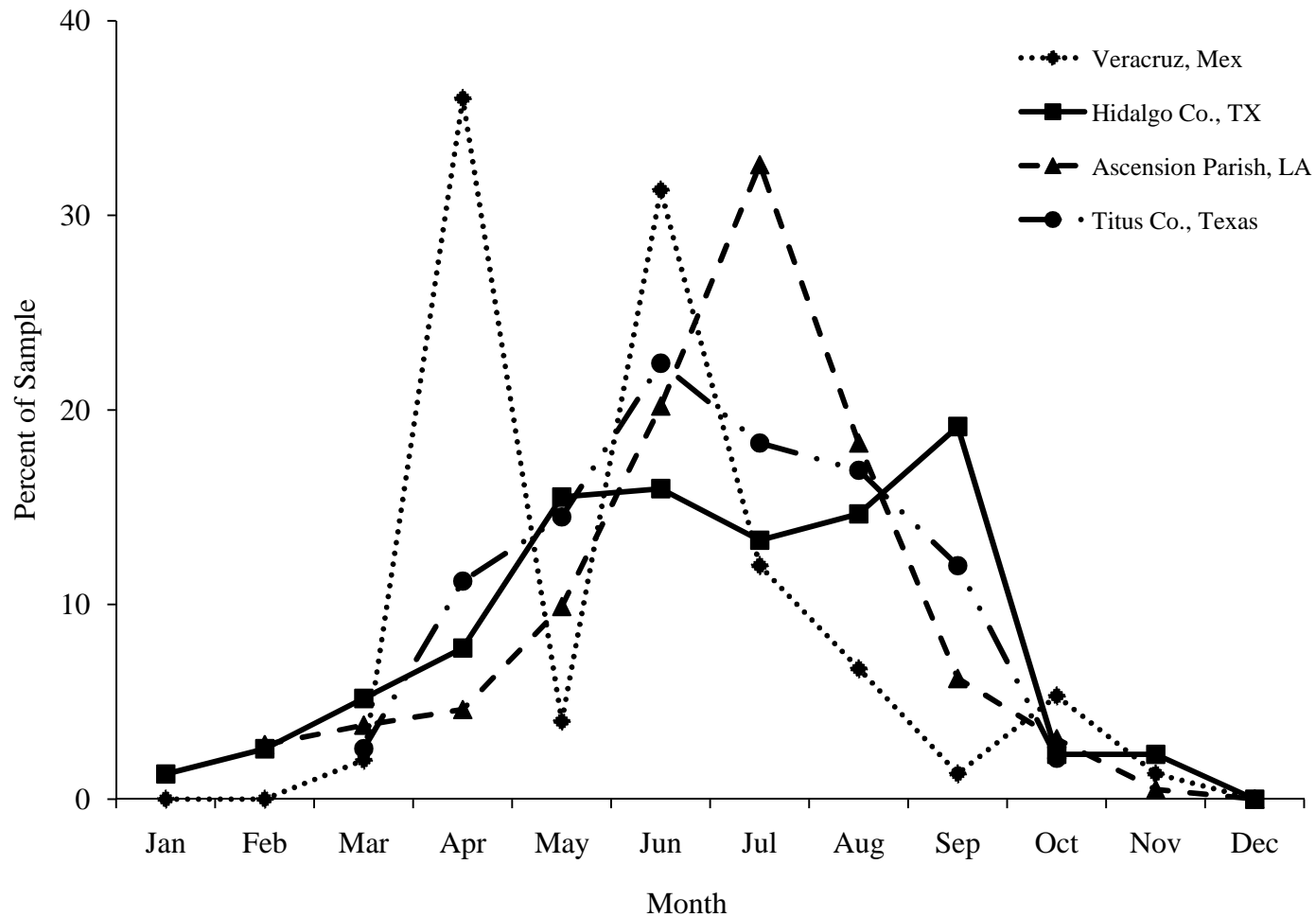


FIG. 25. Comparison of monthly relative abundances among four geographically distinct populations of *Nerodia rhombifer* ranging from tropical Mexico to the northeastern Texas. Effort was made to correct for sampling effort based on information provided in reports for the populations from Veracruz, Mexico (Manjarrez and Garcia, 1991), Ascension Parish, Louisiana (Mushinsky et al. 1980), and Titus County, Texas (Keck, 2004). Data for Hidalgo County, Texas are from this study.

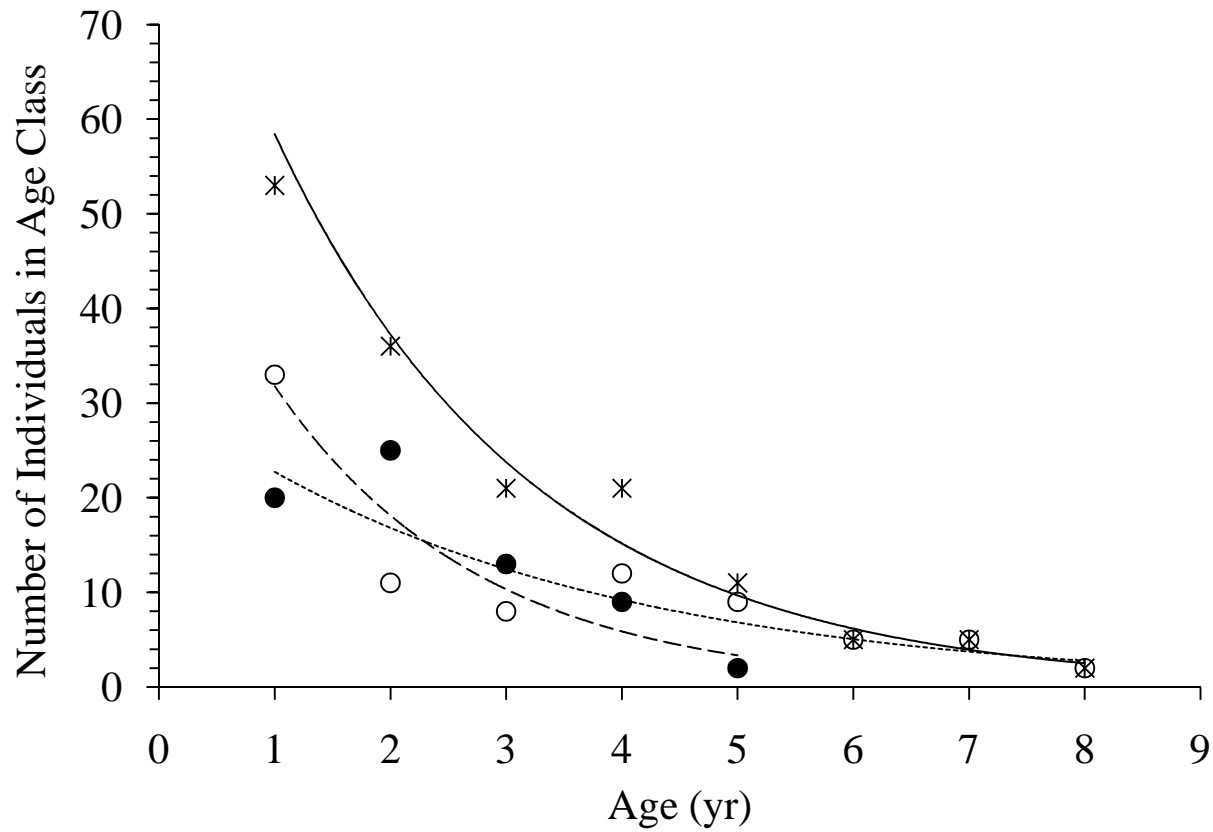


FIG. 26. Survivorship curves for *Nerodia rhombifer* from Willow Lake at Santa Ana National Wildlife Refuge. The groupings were modeled as simple exponential decays that assume constant mortalities after age 1. The regression models were, for females (○ ...),  $y = 30.70e^{-0.30x}$  ( $R^2 = 0.82$ ,  $P = 0.002$ ), males (● --),  $y = 55.81e^{-0.56x}$  ( $R^2 = 0.79$ ,  $P = 0.042$ ), and combined (\* —),  $y = 91.56e^{-0.45x}$  ( $R^2 = 0.97$ ,  $P < 0.001$ ).  $R^2$  = coefficient of determination,  $P$  = probability that the null hypothesis is true.

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## BIOGRAPHICAL SKETCH

Ruben D. Zamora grew up in Linn-San Manuel, a rural community north of Edinburg, Hidalgo County, Texas. After graduating from Edinburg High School, he enrolled at the University of Texas-Pan American (UTPA) as an undeclared major where he was told that eventually he would have to select a course of study. Unsure of a career field, he selected the pre-medical program. For an upper-level biology elective, he took the field-based course “Ornithology” and was hooked. Almost immediately after taking the course, but before completing his undergraduate work, he served as an AmeriCorps volunteer with the U.S. Fish & Wildlife Service assuming duties as a biological technician. It was during this time that he realized that he might be able to earn a living chasing after the critters that he use to when growing up in San Manuel. And, it was during this time that he began the field work for this project. Upon completion of his undergraduate work earning a B.S. in Biology in 1997, he immediately enrolled in the biology graduate program at UTPA. Near the end of his second year of graduate work, a couple of bumps and a fork in the road landed him in a position as a secondary classroom science teacher. Since then he has held various teaching positions and has worked as a natural resource specialist for the Texas Parks & Wildlife Department. He maintains interests in vertebrate ecology, conservation biology, science education, and interpretation of natural history. He currently lives and works in Edinburg and can be contacted at 917 W Stubbs, Edinburg, TX 78539.